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# INTERGENERIC HYBRIDS IN AEGILOPS, TRITICUM, AND SECALE[1]

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## INTRODUCTION

Hybridization of related but widely different forms offers an attractive field for plant improvement. With parents differing in respect to many factors, but still producing hybrids that are fully fertile, abundant material for selection is furnished. With increasing differentiation between the parents, decreasing fertility in the hybrids is likely to result until finally there is complete sterility. It is sometimes assumed that increased differentiation between the parents, up to a point just short of that at which complete sterility in the hybrids is produced, increases the opportunity for obtaining an improved form of plant. Whatever the justification for this view in other species, it has only meager support in the case of wheat. Nevertheless, the method can not be summarily dismissed as offering no possibilities, and, in fact, it has not been, for hybridization of different forms of wheat with one another and with related species proceeds increasingly. As a result, a few segregates of possible value have been obtained in interspecific, and even in intergeneric, crosses, and a considerable body of information regarding the genetic behavior and relationship of the wheat plant and its related forms is being assembled.

The results obtained in an extensive series of hybridization experiments between the several species of the genus Triticum and certain species of the closely related genus Aegilops are presented in this paper. The intention is to record the crosses made, to illustrate and describe briefly the hybrid plants obtained, and to present certain data regarding the fertility and genetics of the hybrids. In addition, previous work in the hybridization of Aegilops and Triticum is reviewed. More detailed studies of the hybrids now under way are reserved for later publication.

## HISTORICAL REVIEW

Aegilops is the generic name applied to a group of plants more or less similar to wheat in appearance and taxonomic characters. The genus includes 12 or more species found growing wild in different parts of the world, but especially in the Mediterranean region. Hybrids between different species of Aegilops and of Triticum have been made by several investigators, and natural hybrids frequently have been observed. In fact, it was on account of this capacity for cross-fertilization that Aegilops was first brought prominently to the attention of botanists. In this a form known as *triticoides* was principally involved.

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In 1821 to 1824 Requien collected specimens of a plant in the environs of Avignon and Nîmes, France, which he described briefly on the herbarium sheets, applying the name *Aegilops triticoides* on account of its resemblance to cultivated wheat. Bertoloni (*3, p. 788–789*)[2] first published the description, and, considering it a new species, applied Requien's name to it. He believed that the plant reported from Italy by Gussone and Tenore under the name *A. triuncialis*, also was *A. triticoides* Req.

In 1838, Esprit Fabre found plants of *Aegilops triticoides* growing in the environs of Agde, France, and with these he immediately began experiments. This fact was communicated to the French Academy of Sciences by Auguste de Sainte-Hilaire (*24*) in 1839, but Fabre (*6*) did not publish his results until 1852.

Fabre found two kinds of plants arising from the seeds of a single spike of *Aegilops ovata*. Of this there could be no doubt, for the old spike, still well preserved, remained attached to the roots of the plants when they were pulled up and examined. One kind of plant had the short compact spike typical of *A. ovata*, and the other had a much larger spike very different from *A. ovata* but identical with the *A. triticoides* of Requien. In 1838, seed from the so-called *A. triticoides*, obtained from the typical *A. ovata*, was sown by Fabre, "in an enclosure surrounded by high walls, far from any place where cereals were cultivated, and in which there was no other gramineous plant." Successive progenies were grown for seven consecutive years in this enclosure. During this time they gradually became more like wheat, until finally he states that "these plants may be regarded as truly Triticum." After five years more in an open, but isolated field, the product is described as a "true wheat (Triticum)"; in this time *A. ovata* had never reappeared. These results led Fabre and others to believe that *A. ovata* is the progenitor of our cultivated wheat.

Fabre observed also that *Aegilops triaristata* Willd. likewise gave rise to the *triticoides* form, but he learned this too late to conduct experiments with it along with those conducted on the form arising from *A. ovata*.

Jordan (*13*), holding views on the immutability of species, questioned the observations and results of Fabre, claiming that he had erred in supposing that *ovata* had changed first to *triticoides* and then to Triticum. In his first discussion of the subject, Jordan favored the view that *triticoides* is a true species, that Fabre had been growing it throughout his experiments, and that the final supposedly wheatlike form was this species. He supposed that this had resulted from a mistake in identification at the beginning. He also advanced the alternate view, which he later (*14*) adopted and maintained, that *Aegilops triticoides*, the form found growing wild in France, was only a sterile modification or deformation of *A. ovata*. The fertile wheatlike plants developed by Fabre were explained as belonging to a rare, unrecorded species, probably native of the Orient, to which he gave the name *A. speltaeformis*. By supposing that confusion in identification had arisen with respect to *A. triticoides* and *speltaeformis* on the one hand, and *speltaeformis* and *Triticum vulgare* on the other, all three forms being much alike yet entirely distinct,

[2] Reference is made by number (italic) to "Literature cited," p. 139.

the phenomena recorded by Fabre and later by others were made to fit his own views. In 1857, Jordan (*15*) defended his position that *triticoides* is only a sterile deformation of *A. ovata*, but admitted that it is due, probably but not certainly, to hybridization. He continued to maintain that *speltaeformis* is a distinct species, and that cultivated wheat does not owe its origin to the wild Aegilops.

Godron (*7*, *8*) repeatedly verified the observations of Fabre as to the origin of *Aegilops triticoides* from seed produced by plants of *A. ovata*. Furthermore, he observed that this form, though never abundant anywhere, was always found only on the borders of wheat fields or in their neighborhood, and only in districts where *A. ovata* occurred as a wild plant. The sudden appearance under these circumstances of a plant with the characteristics of both Triticum and Aegilops, and the fact that it seldom produced seed, led him to question the views of both Fabre and Jordan and to conclude that *triticoides* was a natural hybrid produced by the fertilization of *A. ovata* with wheat pollen.

In order to justify this conclusion, Godron resorted to direct experiment. In 1853, he pollinated several spikes of *Aegilops ovata* with pollen of *Triticum vulgare* and *T. spelta*, respectively, and also several spikes of *A. triaristata* with pollen of *T. durum*. As a result, one or more plants were obtained in each case which were undoubtedly hybrids. They differed in form according to the parentage, but the *A. ovata* × *T. vulgare* hybrid was practically identical with the wild *A. triticoides*. Apparently these plants of Godron were the first artificial hybrids ever made in the grass family, and the natural hybrids found by Requien, Fabre, and others are the first recorded instances of such hybrids in nature. Continuing his experiments, Godron (*9*) crossed *A. ovata* with many different wheats, mostly *T. vulgare* forms but including *T. turgidum* also. In addition he found several natural hybrids in his cultures. On account of the close resemblance of the hybrids, Godron considered the name *triticoides* applicable to the $F_1$ plants of any cross between Aegilops and wheat.

As a result of his experiments and observations, Godron concluded that *triticoides* is self-sterile, but when grown in proximity to wheat under natural conditions, or when again back crossed artificially with wheat, it produced, when fertilization occasionally occurred, the still more wheatlike form to which Jordan had given the name *Aegilops speltaeformis*. Godron grew the *A. speltaeformis* of Fabre in the twenty-sixth generation and the plants were still indefinitely fertile. The anthers were provided with pollen and emerged from the flower in anthesis, as in wheat and *A. ovata*. In 1856, Godron crossed *A. ovata* with the wheat of Agde, a bearded form, and, in 1857, backcrossed the $F_1$ with pollen of the same wheat. In 1858 this produced *A. speltaeformis* similar to that of Fabre, having not only the appearance but all the characters of Fabre's plant, which was being grown in the same garden. Godron grew his *speltaeformis* form for 12 years (to 1869), and it remained constant and similar to Fabre's plant. In the first year (1858) it was only slightly fertile, this agreeing with Fabre's experience, but it was very fertile in the following years. Later crosses with the wheat of Agde (*10*) gave a strain with persistent spikes, as Fabre also had found.

Other wheats than that of Agde when used in crosses with *Aegilops ovata* usually gave results different from the preceding, fertile constant forms seldom being produced. Apparently these latter hybrids were dependent on pollen of wheat for fertilization.

Regel (*21*), in 1853, appears to have been the first to question the conclusion of Fabre that he had transformed Aegilops into wheat. In 1856, Regel (*22, 23*) produced several plants of *Aegilops triticoides* from seeds of *A. ovata* which had resulted from pollination by *Triticum vulgare*. These plants were described as more like wheat than Aegilops, and an examination of the anthers showed only a few pollen grains, nearly all of which were shrunken and poorly developed. Apparently none was capable of fertilizing.

Groenland (*11*), at first working under the direction of Louis de Vilmorin, in 1855 and 1856 hybridized *Aegilops ovata* with *Triticum monococcum*, *T. sativum*, *T. spelta aristata*, and *T. turgidum*. He obtained 11 $F_1$ plants, all but 2 of which were sterile. The cross *A. ovata* × *T. vulgare* was maintained to the $F_3$ generation, and the cross *A. ovata* × *T. turgidum* to the $F_4$ generation, when sterility was complete in each case. Almost always these hybrids had returned to the paternal type, and rarely had maintained their hybrid form. From a seed produced by a natural *triticoides* plant found growing in the vicinity of Agde, Groenland developed another series of hybrids. In this series the fertility increased from generation to generation, the plants grown the fourth year (presumably the $F_5$) being as fertile as cultivated wheat. Plants similar to wheat, appearing in the course of the experiment, were sterile, while those retaining the hybrid or triticoidal form were more or less fertile.

Vilmorin (*34*), after reviewing the work of Louis de Vilmorin and Groenland (*11*), previously cited, reports that his own $F_1$ plants of the cross *Aegilops ovata* × *Triticum vulgare* were sterile.

Bally (*2*) pollinated 250 flowers of *Aegilops ovata* with *Triticum vulgare*, and obtained two $F_1$ plants. From 80 reciprocal pollinations three $F_1$ plants resulted. The reciprocals were similar in appearance. All $F_1$ plants were sterile, their pollen being devoid of starch and otherwise not normally developed. Back crossing the $F_1$ plants with both parental forms failed to produce seed. In a cytological study he found that *T. vulgare* had 8 haploid chromosomes, *A. ovata* 16, and the $F_1$ hybrid 12 or more. The Aegilops chromosomes were more slender than those of *T. vulgare* and could be distinguished in the reduction division. In this connection it should be noted that both Sakamura (*25*) and Sax (*26*) report that *T. dicoccum* has 14 and *T. vulgare* 21 haploid chromosomes. Sax (*27, 28*) reports 14 haploid chromosomes in *A. ovata* and *A. cylindrica*. Percival (*19*) reports 7 haploid chromosomes in *A. cylindrica*, and 14 in *A. ovata* and *A. ventricosa*.

Tschermak (*30, 31, 32*) reports crossing reciprocally several species of wheat with *Aegilops ovata* and *A. cylindrica*, and also *A. ovata* with rye. In most cases the $F_1$ was sterile, the anthers examined being dry, failing to open, and producing no viable pollen. Nevertheless, an occasional kernel developed, especially at the tip of a head. As this occurred only on unprotected heads, natural back crossing with wheat growing near by was possible. However, a small $F_2$ population produced from naturally set seed of the $F_1$ segregated in such a way as to lead Tschermak to the conclusion that the $F_1$ was selfed

rather than backcrossed. Certain $F_2$ plants of the $F_1$ hybrid type also set seed when protected against cross-pollination. This evidence for $F_1$ self-fertility does not appear conclusive, however. Back crossing the $F_1$ with the parental forms very seldom gave any positive result. In contrast to the results of Groenland, the wheatlike plants among the hybrid progenies grown by Tschermak tended to be more fertile than those intermediate in form.

Cook (*5*) describes a wild plant found growing in Palestine which undoubtedly is a hybrid between *Aegilops ovata* and *Triticum dicoccoides* Kcke.

Blaringhem (*4*) crossed *Aegilops ovata* and *A. ventricosa* with *Triticum monococcum* in 1920 and 1921, but states that this was accomplished only with difficulty. Three $F_1$ plants, representing both crosses, were obtained, all of which were sterile, even though repeatedly back crossed with several wheats. In 1921 and 1922 Blaringhem attempted further hybridizations between Triticum, Aegilops, and Secale. In the *A. ventricosa* × *S. cereale* cross two inflated ovaries were obtained. Seeds were obtained in other crosses as follows: *A. ovata* × *T. spelta*, 1 seed and 3 inflated ovaries; *A. ovata* × *T. vulgare*, 1 seed; *A. ovata* × (*T. vulgare* × *T. durum*), 4 seeds; *A. ventricosa* × *T. spelta*, 9 seeds; and *A. ovata* × (*T. monococcum* × *T. durum* fixed hybrid), 13 seeds. At the time of the last report these seeds had not been grown and no data are available regarding them, including whether or not they were actually of hybrid origin. In crosses between Aegilops and wheat, the existence of xenia in the hybrid seed is suggested.

Percival (*18*) reviews much of the work which has been done on Aegilops hybrids. In his opinion a series of crosses initiated long ago between species of Aegilops and wheat of the so-called emmer series could account for the ancestry of *Triticum vulgare* and its allies.

Popova (*20*) reports finding hundreds of natural hybrids between Aegilops and Triticum in Turkestan, in 1921 and 1922 near Tashkent, and in 1922 also not far from Jan-Aryk. Several species of Aegilops are found there in abundance, growing wild on untilled land near wheat fields and to some extent in the fields themselves. Two groups of these hybrids are described, whose respective characters indicate the following parentage: *A. cylindrica* Host. × *T. vulgare* L., and *A. crassa* Bois × *T. vulgare* L. Complete sterility apparently existed in all but eight or nine plants, from one of which two seeds were obtained, while the others produced only one seed each. Only three $F_2$ plants were grown, two being like *A. cylindrica* and one like the hybrid.

## METHODS AND MATERIALS

The results of an extensive series of hybridizations of two species of Aegilops, viz, *ovata* and *triuncialis*, with members of different groups of Triticum,[3] and also with *Secale cereale*, are reported in this paper. *A. ovata* was crossed with one or more varieties each of *T. monococcum*, *T. dicoccum*, *T. dicoccoides*, *T. durum*, *T. polonicum*, *T. turgidum*, *T. compactum*, *T. spelta*, and *T. vulgare*, and also with *S. cereale*. *A. triuncialis* was crossed with all the forms named except *T. monococcum*. *A. ventricosa* was used in a few of the cases reported here.

[3] The groups of Triticum named below will be referred to hereafter as species.

Aegilops is described by Ascherson and Graebner (*1, p. 703–714*) and others as a group of plants comprising 12 species indigenous to southern Europe, and western Asia as far as Afghanistan and Turkestan; low annuals with bent stems; spikes short, varying in shape from ovate to oblong or elongate cylindrical; spikelets with three or more flowers, glumes hard and tough, many nerved, indistinctly or not at all keeled, usually with two to many awns or teeth; lemmas leathery, with one to three awns or teeth.

Aegilops was known to the ancients, and in regions where it was indigenous it was used at a very remote period as an important article of food. At present Aegilops is apparently of no economic importance anywhere. One species, *A. cylindrica*, has recently been reported in the United States from Oklahoma, Kansas, and Washington. In the first two States it is found as a weed in wheat fields, apparently having been introduced with wheat seed from Russia. In Washington it is supposed to have escaped from a botanical garden.

Considerable divergence of opinion has existed among botanists with respect to the proper classification of Aegilops. Linnaeus (*16*) established Aegilops as a genus and named five species. Hackel (*12*) divided the genus Triticum into two sections, Aegilops and Sitopyrus, the latter including the true wheats. Ascherson and Graebner (*1, p. 703–714*) unite Aegilops and wheat in the genus Triticum. It appears to the present writers that Aegilops and Triticum are differentiated by characters of sufficient taxonomic importance to be considered as separate genera. This is despite the fact that hybridizations are accomplished rather readily between certain members of the two groups, and that self-fertility occasionally occurs in such hybrids.

Aegilops is regarded as a genus parallel to Triticum. As such, the characters of one reappear in homologous series in the other, as has been pointed out by Vavilov (*33*) for several genera. There is also a general resemblance between certain species in each genus. Vavilov states:

> The genus Aegilops, which is related to Triticum, and grows in large quantities in natural wild conditions in southern Russia, Turkestan and Persia, as was shown by our observations, repeats in general all varieties of the genus Triticum. In *Aegilops squarrosa* and *Ae. cylindrica*, there are beardless as well as bearded varieties, varieties with yellow, red and black ears, hairy and smooth ears; and we know winter as well as spring varieties of these Linneons. The same division of the genus Aegilops into collective Linneons seems to be similar to that of *Eutriticum* (cultivated wheats). The Linnean species, *Aegilops cylindrica* and *Ae. squarrosa*, are akin to *Triticum vulgare* and to other Linneons of the same group of wheat. Both are characterized in general by hollow stems, susceptibility to yellow and brown rusts (*Puccinia glumarum* and *P. triticina*), to mildew (*Erysiphe graminis*), and to smut—*Tilletia tritici*. Other Linneons, like *Aegilops triuncialis*, correspond more to *Triticum durum* or *T. monococcum* in their immunity to these parasites, and the similarity of their straw, which is full of pith, and in the absence of completely beardless varieties.
>
> As is known, Godron artificially produced hybrids of wheat and Aegilops, which proves the relative affinity of these genera.

Popova (*20*) makes the following statement:

> We find for the typical wild growing species of Aegilops a complete parallelism in variability with the cultivated species of the genus Triticum.

Stapf (*29*) states that he has seen specimens of *A. cylindrica* very similar in spike characters to *T. spelta*. Percival (*18*) furnishes illustrations of spikes of *A. cylindrica* and *T. spelta* showing the

resemblance in certain head characters. On these accounts it is difficult to taxonomically differentiate the two groups, Aegilops and Triticum. However, similar difficulty is encountered in differentiating Triticum from Secale and Agropyron.

The glumes of Aegilops are only slightly keeled or not at all, as contrasted with the always more or less distinctly keeled glumes of Triticum. In seed characters the different species of Aegilops and wheat are somewhat similar, although the seeds of all of the Aegilops described remain firmly inclosed in the glumes when threshed. In this they resemble einkorn, emmer, and spelt among the wheats; yet one familiar with these plants would hardly confuse the covered or naked seeds of any of the species concerned. In the general appearance and in many detailed characters of the Aegilops plants the same situation exists for the most part. Resemblances to Triticum are apparent, but usually little difficulty is experienced in properly placing the several forms.

The first plants of Aegilops raised in connection with the experiments reported herein belonged to the species *triuncialis*, the seeds of which were found in an introduction (Foreign Seed and Plant Introduction No. 29026) of wheat from Palestine in 1912. Since then the species *ovata*, *ventricosa*, *cylindrica*, and *speltoides* have been grown. In Figures 1 and 2 are shown representative plants of *ovata* and *triuncialis*. The leaves of these two latter species, as grown in these experiments, are narrow and abundantly hairy on both surfaces. Hairs are also found on the leaf sheaths. The height of these two species is less than half that of the average wheat. *A. triuncialis* has two to three long awns on the glumes, and very slender, lax heads with three to six spikelets each. *A. ovata* has four to seven shorter awns on the glumes, and a short, denser spike with usually three to five spikelets, only the two lower of which usually are fertile. At maturity the spikes of both of these species disarticulate at a point on the rachis below the lowest perfect spikelet. The spike remains entire and does not break up naturally into separate spikelets, as is the case in several other species of Aegilops.

In making crosses on Aegilops usually the distal spikelet of *ovata* and one or two of the uppermost spikelets of *triuncialis* were removed. Only the two lower flowers in the remaining spikelets were used for crossing, the upper flowers being entirely removed. The anthers were removed from the flowers while they were still green, and, after emasculation, the head was protected with a glassine bag. The pollen was applied to the stigmas from two to five days after emasculation. Bags were replaced after pollination was completed. In reciprocal crosses on wheat the process of hybridizing was practically the same. The number of flowers pollinated per head usually was from 18 to 24 in wheat, 4 in *ovata*, and 6 to 8 in *triuncialis*. Practically all of the crosses have been made in the greenhouses of the United States Department of Agriculture at Arlington Experiment Farm, near Washington, D. C., and nearly all of the hybrids as well as the parental forms, especially of Aegilops, also have been grown in these greenhouses.

The data taken on the fertility of the hybrids were confined to a consideration of the two lower flowers of each spikelet on a head.

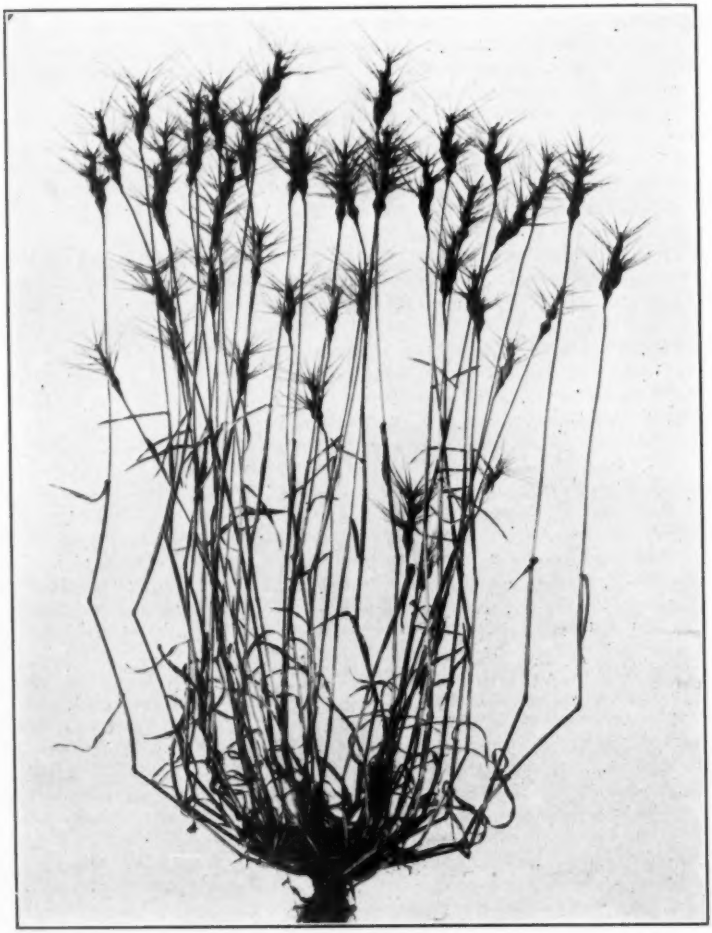

FIG. 1.—Plant of *Aegilops ovata*

FIG. 2.—Plant of *Aegilops triuncialis*

## HYBRIDIZATIONS MADE

### EARLIER EXPERIMENTS

The first attempt at hybridizing wheat and Aegilops in connection with these studies was made in 1913, when 146 flowers of common wheat (*Triticum vulgare*) and 8 flowers of Polish wheat (*T. polonicum*) were emasculated and pollinated with *A. triuncialis*. Six kernels were produced from the *T. vulgare* cross, but none from the *T. polonicum*. In the following year two plants were raised from these kernels, both of which were sterile. No attempts were made

FIG 3.—Spikes: *A, Aegilops triuncialis; B, F₁ Triticum vulgare* ♀ × *Aegilops triuncialis* ♂; *C, Triticum vulgare* (New Columbia)

to back cross the hybrids with parental forms. Figure 3 shows the first Aegilops-wheat cross made at Arlington. As far as the writers are aware this is the first report of an artificial hybrid between *A. triuncialis* and *Triticum*. Loret (*17*) reports that he had examined two or three incomplete specimens among the plants of M. Martin of Bédarieux which he (Loret) believed to be a hybrid between *A. triuncialis* and *T. vulgare*.

In 1918 the following crosses were attempted:

PARENTS

| | |
|---|---|
| Aegilops ovata × Triticum vulgare: | |
| Flowers pollinated | 12 |
| Kernels obtained | 7 |
| Aegilops triuncialis × Triticum vulgare: | |
| Flowers pollinated | 6 |
| Kernels obtained | 1 |
| Aegilops ovata × Secale cereale: | |
| Flowers pollinated | 6 |
| Kernels obtained | 4 |
| Aegilops triuncialis × Secale cereale: | |
| Flowers pollinated | 6 |
| Kernels obtained | 0 |

The four seeds obtained from *Aegilops ovata* × *Secale cereale* failed to germinate. One plant of the cross *A. triuncialis* × *Triticum vulgare*, and four plants of the *A. ovata* × *T. vulgare* cross matured in the greenhouse in 1920, all of which were again self-sterile. Backcrossing with wheat also failed.

The following crosses were made in the greenhouse in 1920:

PARENTS

| | |
|---|---|
| Aegilops ovata × Secale cereale: | |
| Flowers pollinated | 72 |
| Kernels obtained | 9 |
| Triticum vulgare × Aegilops ventricosa: | |
| Flowers pollinated | 26 |
| Kernels obtained | 4 |

Two $F_1$ plants were produced from the cross *Aegilops ovata* × *Secale cereale* and one from the cross *Triticum vulgare* × *Aegilops ventricosa*. All three hybrids were self-sterile, and backcrossing with rye and wheat failed to produce seed.

## LATER HYBRIDIZATION EXPERIMENTS

In 1921, a series of experiments was initiated involving the hybridization of *Aegilops* with wheat on a more extensive scale. Crosses between most of the species of wheat and two species of *Aegilops*, viz, *ovata* and *triuncialis*, were attempted. The crosses, made principally in 1921, between *A. ovata* and *A. triuncialis*, and different species of Triticum are listed in Table 1, together with data on numbers of flowers pollinated, seeds obtained, and plants matured.

TABLE 1.—*List of hybridizations attempted and accomplished between species of Aegilops and Triticum, with data on heads and flowers pollinated, seed obtained, and $F_1$ plants matured*

| Hybrid combination and parental wheat variety | C. I. No. | Number of heads worked | Number of flowers pollinated | Seed obtained | | Number of $F_1$ plants matured |
|---|---|---|---|---|---|---|
| | | | | Number | Per cent | |
| A. ovata × T. monococcum: | | | | | | |
| Einkorn | ------ | 9 | 54 | 7 | 13.0 | 1 |
| A. ovata × T. dicoccum: | | | | | | |
| Khapli | 4013 | 7 | 34 | 8 | 23.5 | 5 |
| Black Winter | 2337 | 6 | 24 | 6 | 25.0 | 6 |
| Total | ------ | 13 | 58 | 14 | 24.1 | 11 |
| A. ovata × T. dicoccoides: | | | | | | |
| Wild | 3109 | 8 | 32 | 7 | 21.9 | 4 |
| A. ovata × T. durum: | | | | | | |
| Kubanka | 1440 | 5 | 28 | 7 | 25.0 | 2 |
| Kahla | 5529 | 1 | 6 | 5 | 83.3 | 3 |
| Pentad | 3322 | 2 | 8 | 5 | 62.5 | 4 |
| Arnautka | 1494 | 1 | 4 | 3 | 75.0 | 2 |
| Total | ------ | 9 | 46 | 20 | 43.5 | 11 |
| T. durum × A. ovata: | | | | | | |
| Golden Ball | 6227 | 1 | 18 | 0 | .0 | 0 |
| Kubanka | 1440 | 2 | 49 | 2 | 4.1 | 2 |
| Total | ------ | 3 | 67 | 2 | 3.0 | 2 |
| A. ovata × T. polonicum: | | | | | | |
| White Polish | 3007 | 7 | 34 | 13 | 38.2 | 9 |
| A. ovata × T. turgidum: | | | | | | |
| Alaska | 5988 | 5 | 26 | 18 | 69.2 | 9 |
| Clackamas | 6241 | 1 | 4 | 4 | 100.0 | 2 |
| Total | ------ | 6 | 30 | 22 | 73.3 | 11 |
| A. ovata × T. compactum: | | | | | | |
| Dale Gloria | 4155 | 3 | 16 | 11 | 68.8 | 3 |
| Little Club | 4066 | 1 | 6 | 3 | 50.0 | 0 |
| Mayview | 5874 | 3 | 14 | 6 | 42.9 | 0 |
| Coppei | 3088 | 2 | 8 | 5 | 62.5 | 0 |
| Big Club | 4257 | 1 | 4 | 2 | 50.0 | 1 |
| Total | ------ | 10 | 48 | 27 | 56.3 | 4 |
| T. compactum × A. ovata: | | | | | | |
| Blue Chaff | 5256 | 2 | 40 | 0 | 0 | 0 |
| Jenkins | 5177 | 1 | 16 | 0 | 0 | 0 |
| Total | ------ | 3 | 56 | 0 | 0 | 0 |
| A. ovata × T. spelta: | | | | | | |
| White Bearded | 1774 | 5 | 24 | 8 | 33.3 | 3 |
| Alstroum | 1773 | 6 | 30 | 14 | 46.7 | 5 |
| Total | ------ | 11 | 54 | 22 | 40.7 | 8 |
| A. ovata × T. vulgare: | | | | | | |
| Grandprize | 4876 | 1 | 6 | 2 | 33.3 | 1 |
| Satisfaction | 3588 | 4 | 20 | 8 | 40.0 | 2 |
| Hard Federation | 4980 | 2 | 10 | 5 | 50.0 | 1 |
| Canadian Red | 6282 | 3 | 14 | 8 | 57.1 | 4 |
| Propo | 1970 | 1 | 4 | 2 | 50.0 | 0 |
| Sonora | 3336 | 2 | 8 | 7 | 87.5 | 3 |
| Jones Fife | 4468 | 1 | 4 | 2 | 50.0 | 0 |
| Pacific Bluestem | 4067 | 1 | 6 | 2 | 33.3 | 0 |
| Allen | 5407 | 1 | 4 | 4 | 100.0 | 2 |
| Kanred | 5146 | 2 | 10 | 3 | 30.0 | 0 |
| ——— | 6629 | 2 | 8 | 5 | 62.5 | 1 |
| Champlain | 4782 | 1 | 6 | 4 | 66.7 | 0 |
| $F_1$ Fultz × C. I. No. 6193 | ——— | 1 | 4 | 4 | 100.0 | 1 |
| Preston | 3328 | 1 | 4 | 4 | 100.0 | 0 |
| Purplestraw | 1915 | 3 | 12 | 11 | 91.7 | 3 |
| Stanley | 4796 | 1 | 4 | 4 | 100.0 | 3 |
| Kofod | 4337 | 1 | 4 | 4 | 100.0 | 3 |
| Ladoga | 4795 | 2 | 8 | 7 | 87.5 | 5 |
| Humpback | 3690 | 1 | 4 | 4 | 100.0 | 2 |
| Trumbull | 5657 | 1 | 4 | 3 | 75.0 | 1 |

TABLE 1.—*List of hybridizations attempted and accomplished between species of Aegilops and Triticum, with data on heads and flowers pollinated, seed obtained, and $F_1$ plants matured*—Continued

| Hybrid combination and parental wheat variety | C. I No. | Number of heads worked | Number of flowers pollinated | Seed obtained | | Number of $F_1$ plants matured |
|---|---|---|---|---|---|---|
| | | | | Number | Per cent | |
| A. ovata × T. vulgare—Continued. | | | | | | |
| Rising Sun | 5977 | 2 | 8 | 0 | 0 | 0 |
| Red Chaff | 4241 | 1 | 4 | 1 | 25.0 | 0 |
| 2090a-1 | ------ | 1 | 4 | 4 | 100.0 | 1 |
| Total | ------ | 36 | 160 | 98 | 61.3 | 33 |
| T. vulgare × A. ovata: | | | | | | |
| Marquis | 3641 | 1 | 24 | 3 | 12.5 | 3 |
| Walker | 6445 | 1 | 14 | 0 | 0 | 0 |
| Total | ------ | 2 | 38 | 3 | 7.9 | 3 |
| A. triuncialis × T. dicoccum: | | | | | | |
| Khapli | 4013 | 3 | 20 | 5 | 25.0 | 5 |
| A. triuncialis × T. dicoccoides: | | | | | | |
| Wild | 3109 | 3 | 22 | 9 | 40.9 | 7 |
| T. dicoccoides × A. triuncialis: | | | | | | |
| Wild | 3109 | 2 | 30 | 0 | 0 | 0 |
| A. triuncialis × T. durum: | | | | | | |
| Peliss | 1584 | 1 | 10 | 8 | 80.0 | 4 |
| T. durum × A. triuncialis: | | | | | | |
| Kubanka | 1440 | 1 | 26 | 6 | 23.1 | 0 |
| A. triuncialis × T. polonicum: | | | | | | |
| White Polish | 3007 | 1 | 6 | 1 | 16.7 | 1 |
| A. triuncialis × T. turgidum: | | | | | | |
| Alaska | 5988 | 1 | 6 | 2 | 33.3 | 2 |
| Titantic | 5535 | 1 | 8 | 0 | 0 | 0 |
| Total | ------ | 2 | 14 | 2 | 14.3 | 2 |
| A. triuncialis × T. compactum: | | | | | | |
| Dale Gloria | 4155 | 1 | 6 | 5 | 83.3 | 5 |
| T. compactum × A. triuncialis: | | | | | | |
| Blue Chaff | 5256 | 1 | 4 | 1 | 25.0 | 0 |
| Jenkin | 5177 | 1 | 12 | 2 | 16.7 | 0 |
| Dale Gloria | 4155 | 1 | 10 | 1 | 10.0 | 0 |
| Total | ------ | 3 | 26 | 4 | 15.4 | 0 |
| A. triuncialis × T. spelta: | | | | | | |
| White Bearded Spelt | 1774 | 2 | 12 | 4 | 33.3 | 4 |
| A. triuncialis × T. vulgare: | | | | | | |
| Prelude | 4323 | 1 | 4 | 4 | 100.0 | 1 |
| Hard Federation | 4980 | 1 | 8 | 6 | 75.0 | 5 |
| Canadian Red | 6282 | 1 | 8 | 5 | 62.5 | 5 |
| Sonora | 3036 | 2 | 12 | 6 | 50.0 | 5 |
| Grandprize | 4876 | 1 | 6 | 4 | 66.7 | 2 |
| Rink | 5868 | 1 | 6 | 2 | 33.3 | 1 |
| Total | ------ | 7 | 44 | 27 | 61.4 | 19 |
| T. vulgare × A. triuncialis: | | | | | | |
| Rising Sun | 5977 | 1 | 22 | 3 | 13.6 | 1 |
| Walker | 6445 | 1 | 22 | 0 | 0 | 0 |
| Purplestraw | 1915 | 1 | 18 | 2 | 11.1 | 1 |
| Total | ------ | 3 | 62 | 5 | 8.1 | 2 |

## HYBRIDS BETWEEN AEGILOPS OVATA AND TRITICUM SPECIES

In Table 1 the crosses made between *Aegilops ovata* and different wheat forms are listed first, and following these are the crosses in which *A. triuncialis* was used. The different combinations will be considered in the order in which they appear in the table, the first being that between *A. ovata* and *Triticum monococcum*. Only one variety of *monococcum* was used, pollen of which was applied to 54 flowers of *ovata*. As a result seven seeds were obtained, from which

one plant was produced. A spike from one of these plants, together with spikes of the parents, are shown in Figure 4. The resemblance of this $F_1$ plant to the *monococcum* parent is quite striking. The $F_1$ plant was 26 inches in height, and the *monococcum* parent 30 inches.

Two varieties of emmer (*Triticum dicoccum*), Khapli and Black Winter, were used as pollen parents in crosses with *A. ovata*. A total of 58 flowers was pollinated, of which 14, or 24.1 per cent, produced seed. From these, 11 $F_1$ plants were produced, a spike from one of which is shown in Figure 5, together with a spike of Khapli emmer. This is one of the few hybrids between *A. ovata* and Triticum from which seeds were obtained by selfing.

FIG. 4.—Spikes: *A, Aegilops ovata; B,* $F_1$ *Aegilops ovata* ♀ × *Triticum monococcum vulgare* ♂; *C, Triticum monococcum vulgare*

When *Aegilops ovata* was crossed with the so-called "wild wheat of Palestine" (*Triticum dicoccoides*), seven, or 21.9 per cent, of the 32 flowers pollinated produced seeds. From these, four $F_1$ plants were grown. A spike of one of these is shown in Figure 5 together with a spike of *T. dicoccoides*.

Four varieties of durum wheat (*Triticum durum*) were used as the pollen parent in crosses with *Aegilops ovata*, 46 flowers being pollinated of which 20, or 43.5 per cent, produced seeds. Eleven $F_1$ plants were obtained, a spike of one of which is shown in Figure 6, together with spikes of the parental forms, *ovata* and Kubanka durum. The $F_1$ of this cross was vigorous, and was self-fertile to a slight degree. The $F_1$ of the cross in which Arnautka durum was used as the pollen parent was considerably more self-fertile than the cross with Kubanka.

In the reciprocal of the above cross, 67 flowers of 2 varieties of durum pollinated by *Aegilops ovata* produced only 2 seeds, or a percentage of 3.0. These were produced by Kubanka, the crosses on Golden Ball being unsuccessful.

Polish wheat (*Triticum polonicum*) was used to pollinate 34 flowers of *A. ovata*, of which 13, or 38.2 per cent, produced seeds. From these

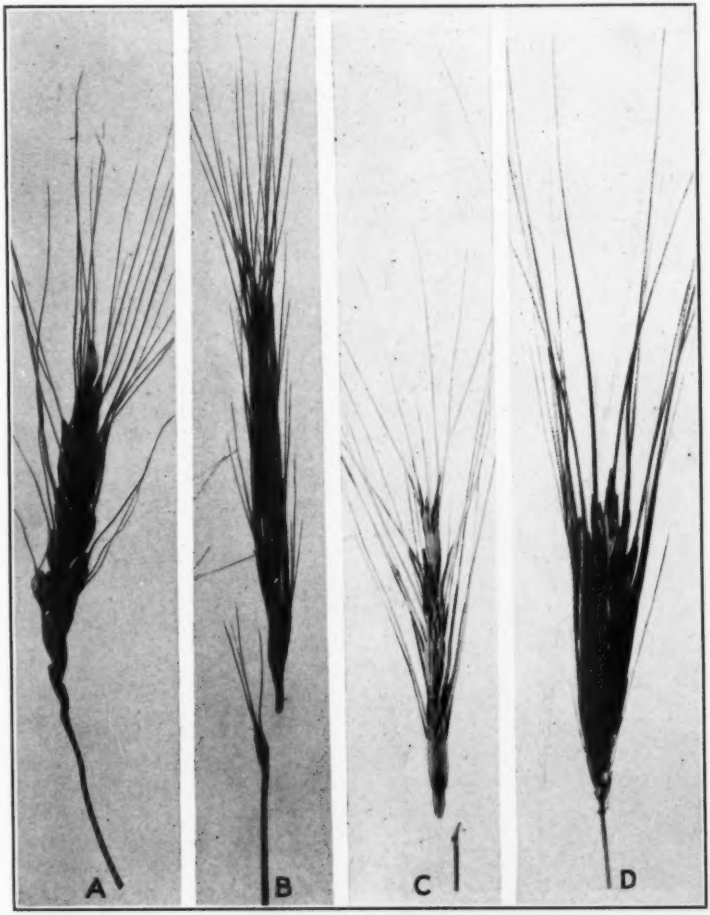


FIG. 5.—Spikes: *A*, *Triticum diococcum* (Khapli); *B*, $F_1$ of *Aegilops ovata* ♀ × *Triticum diococcum* ♂; *C*, $F_1$ of *Triticum dicoccoides* ♀ × *Aegilops ovata* ♂; *D*, *Triticum dicoccoides*

nine $F_1$ plants were obtained. A spike of one of these is shown in Figure 7, together with a spike of each of the parents. The influence of the Polish parent in increasing the glume length of the hybrid is apparent when the $F_1$ of this cross is compared with the $F_1$ of other combinations illustrated. The $F_1$ was almost completely sterile. White Polish, the wheat parent, however, was partially sterile when grown in the same environment as the hybrids.

Two varieties of *Triticum turgidum*, Alaska and Clackamas, were used in crosses with *Aegilops ovata*, a total of 30 flowers being pollinated. Of these 22, or 73.3 per cent, produced seed. Eleven $F_1$

FIG. 6.—Spikes: *A*, *Aegilops ovata*; *B*, $F_1$ of *Aegilops ovata* ♀ × *Triticum durum* ♂; *C*, *Triticum durum* (Kubanka)

plants were obtained, a spike of one of which is shown in Figure 8, together with spikes of the parental forms, *A. ovata* and Alaska wheat. The $F_1$ was self-sterile, but set seed when pollinated with wheat.

Five varieties of club wheat (*Triticum compactum*) were used as the pollen parent in crosses with *Aegilops ovata*. From the 48 flowers pollinated, 27 seeds were obtained, or 56.3 per cent. A spike of the

FIG. 7.—Spikes: *A*, *Aegilops ovata*; *B*, $F_1$ of *Aegilops ovata* ♀ × *Triticum polonicum* ♂; *C*, *Triticum polonicum* (White Polish)

$F_1$ and of each of the parents, *ovata* and Dale Gloria, is shown in Figure 8. The lax hybrid head shows little or no influence of the compact-headed wheat parent, in respect to head shape. The $F_1$ plant was dwarfed and stunted in growth and late in maturing. The fully developed plant was shorter even than the *ovata* parent,

and it was completely sterile. Two different varieties of club wheat were used as the female parent in crosses with *ovata*, but no seed was obtained in 56 attempts.

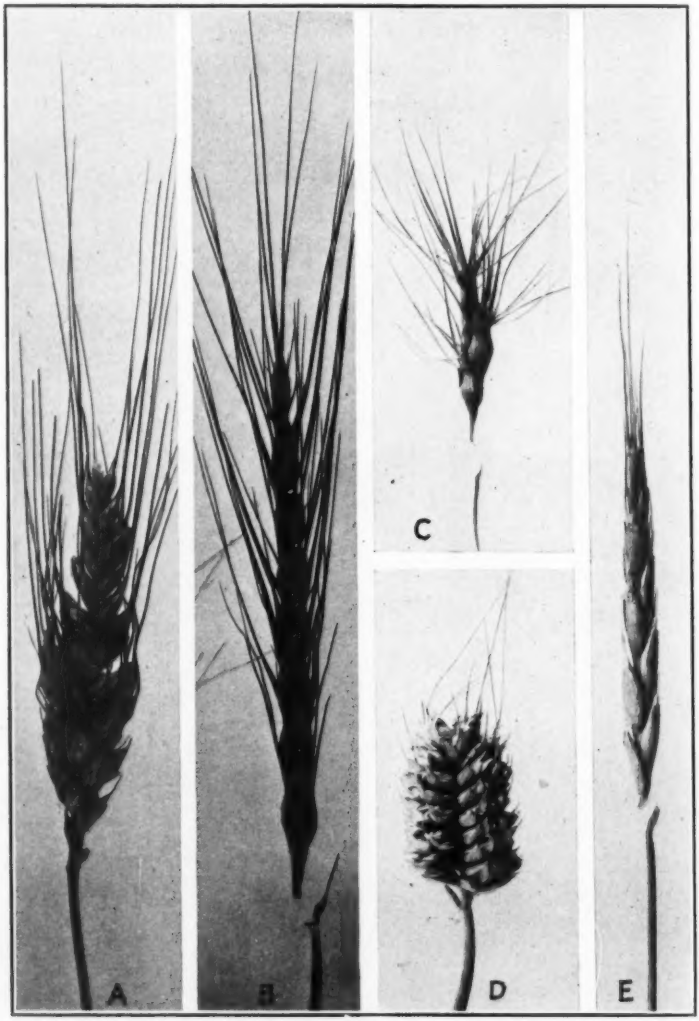


FIG. 8.—Spikes: *A*, *Triticum turgidum* (Alaska); *B*, $F_1$ of *Aegilops ovata* ♀ × *Triticum turgidum* ♂; *C*, *Aegilops ovata*; *D*, *Triticum compactum* (Dale Gloria); *E*, $F_1$ *Aegilops ovata* ♀ × *Triticum compactum* ♂.

Two varieties of spelt (*Triticum spelta*), White Bearded and Alstroum, were used in crosses on *Aegilops ovata*. From the 54 flowers pollinated, 22 seeds were obtained, a percentage of 40.7. Eight $F_1$ plants were produced, of which a spike is shown in Figure 9, together with

*Aegilops ovata* and White Bearded spelt, the parents. The $F_1$ of this hybrid was self-sterile, but a few seeds were produced when wheat (*Triticum vulgare*) pollen was used for fertilization.

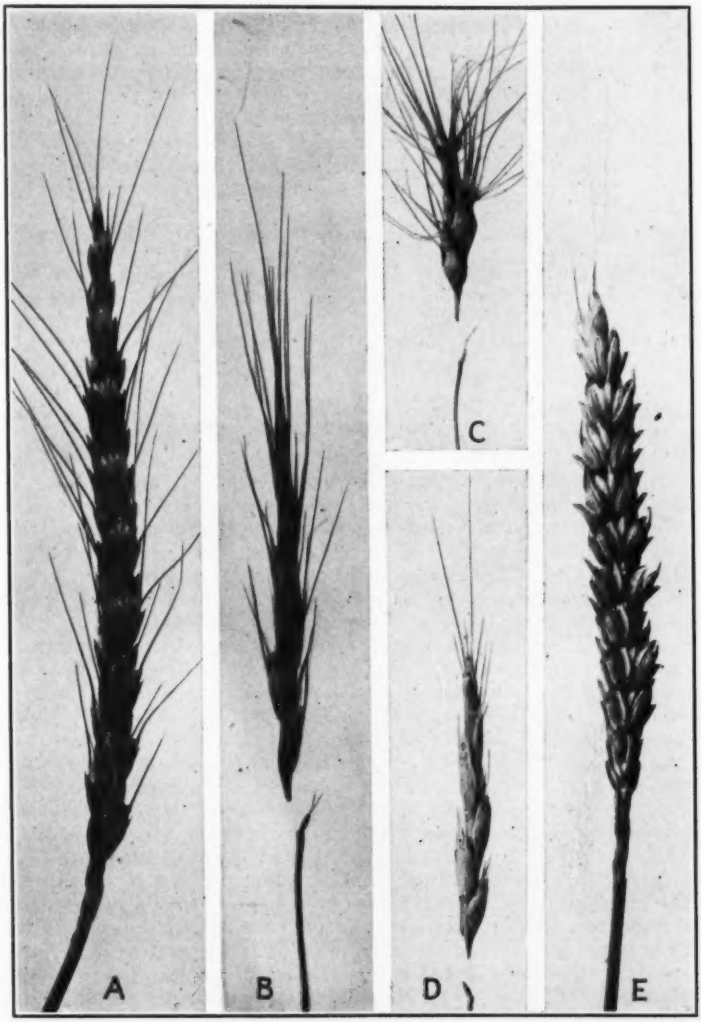


FIG. 9.—Spikes: *A*, *Tricitum spelta* (White Bearded); *B*, $F_1$ of *Aegilops ovata* ♀ × *Triticum spelta* ♂; *C*, *Aegilops ovata*; *D*, $F_1$ of *Aegilops ovata* ♀ × *Triticum vulgare* ♂; *E*, *Triticum vulgare* (Purple-straw)

The most extensive series of hybrids between *Aegilops ovata* and the different wheat groups is that in which *Triticum vulgare* was used. Of the latter, 23 different strains or varieties were used as the pollen parent in crosses on *ovata*. A wide range of types is represented

in these strains, including winter and spring, white-kerneled and red-kerneled, hard red and soft red, varieties adapted to the most diverse climates and conditions, and varieties differing in many morphological characters. Of the 160 *ovata* flowers pollinated with these various strains, 98, or 61.3 per cent, produced seed. In the case of only one strain was no seed produced, all other crosses resulting in from 25 to 100 per cent fertility. The reciprocal cross, in which *ovata* furnished the pollen, was attempted on only 38 flowers of two varieties of *T. vulgare*. From these only 3 seeds were obtained, or 7.9 per cent.

From the 101 seeds produced in the crosses between *Aegilops ovata* and *Triticum vulgare*, 36 $F_1$ plants were grown. A spike of the *ovata* × Purplestraw cross, and of each of the parents, is shown in Figure 9.

### Hybrids Between Aegilops triuncialis and Triticum Species

*Aegilops triuncialis* was crossed with one variety of *Triticum dicoccum*, the Khapli emmer. From the 20 flowers pollinated, five seeds were obtained, a percentage of 25. From these seeds 5 plants were obtained. A spike of one of these $F_1$ plants and spikes from the two parents are shown in Figure 10. This hybrid showed slight self-fertility.

Reciprocal crosses were attempted between *Aegilops triuncialis* and the "wild wheat of Palestine" (*Triticum dicoccoides*). From the 22 flowers pollinated by the wild emmer, 9 seeds were obtained, or 40.9 per cent. No seed was obtained from the reciprocal cross. From the nine seeds, seven $F_1$ plants were produced, a spike of the $F_1$ being shown in Figure 10 together with spikes of the parental forms. This hybrid was exceptionally vigorous and produced selfed seed.

Durum wheat (*Triticum durum*) was used in reciprocal crosses with *Aegilops triuncialis*. When Peliss durum was used as the pollen parent, 8 seeds were obtained from 10 flowers pollinated, a percentage of 80. From these, four plants were produced. In the reciprocal cross, in which Kubanka durum was used as the female parent, 26 flowers produced 6 seeds, a percentage of 23.1. From these seeds no plants were obtained. A spike of the $F_1$ hybrid between *triuncialis* and Peliss durum, and spikes of the parents, are shown in Figure 11. The $F_1$ of this cross also was vigorous and self-fertile. The $F_1$ spike was somewhat speltlike in appearance.

Only one seed was obtained from six flowers of *Aegilops triuncialis* pollinated by Polish wheat (*Triticum polonicum*), a percentage of 16.7. From this single seed a plant was grown, which was completely sterile. The spike of this $F_1$ plant, shown with parental spikes in Figure 11, exhibits some influence of the Polish parent in the character of the glumes.

Two varieties of *Triticum turgidum*, Alaska and Titanic, were used for pollinating *Aegilops triuncialis*. None of the 8 flowers pollinated by Titanic produced seed, but 2 seeds were obtained from 6 flowers pollinated by Alaska, a percentage of 33.3. From these seeds 2 plants were grown, which were highly self-fertile, producing a total of 44 seeds. Spikes of the hybrid and of the parents are shown in Figure 12.

Three varieties of club wheat (*Triticum compactum*) were used in crosses with *Aegilops triuncialis*. When Dale Gloria was used as the pollen parent, five seeds were produced by six flowers pollinated, a percentage of 83.3. This variety and two others when used as

the female parents in crosses with *triuncialis*, produced four seeds from 26 flowers, a percentage of 15.4. From these four seeds no plant was obtained, but five plants were obtained from the five seeds obtained in the *triuncialis* × Dale Gloria cross. A spike from one of these, together with the parents, is shown in Figure 12. The

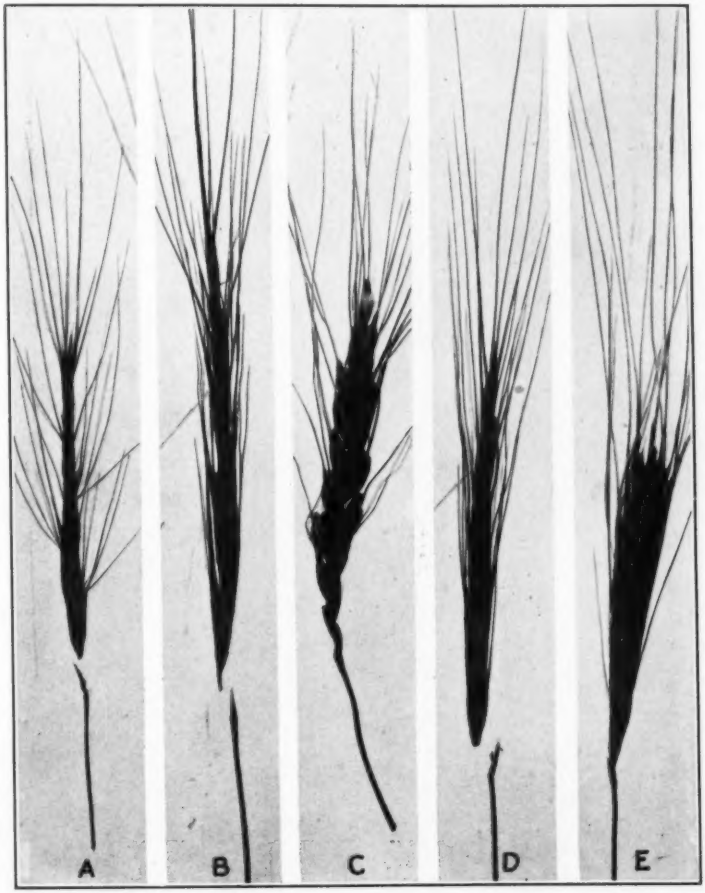


FIG. 10.—Spikes: *A*, *Aegilops triuncialis*; *B*, $F_1$ of *Aegilops triuncialis* ♀ × *Triticum dicoccum* ♂; *C*, *Triticum dicoccum* (Khapli); *D*, $F_1$ of *Aegilops triuncialis* ♀ × *Triticum dicoccoides* ♂; *E*, *Triticum dicoccoides*

influence of the wheat parent on head shape is evident in this $F_1$, the spike obtained in this cross being the most compact obtained in any of the crosses with *triuncialis*, as the wheat parent is also the most compact wheat used. The $F_1$ of this cross was quite vigorous and was both self-fertile, although only slightly so, and productive of seed when backcrossed with wheat pollen.

White Bearded spelt was the only variety of *Triticum spelta* used in a cross with *Aegilops triuncialis*, 12 flowers of the latter producing 4 seeds, a percentage of 33.3. From these seeds four plants were produced, of which a spike, together with the parents, is shown in Figure 13. This hybrid showed slight fertility, both when selfed and when backcrossed with pollen of common wheat.

FIG. 11.—Spikes: *A*, *Aegilops triuncialis*; *B*, $F_1$ of *Aegilops triuncialis* ♀ × *Triticum durum* ♂; *C*, *Triticum durum* (Peliss); *D*, $F_1$ of *Aegilops triuncialis* ♀ × *Triticum polonicum* ♂; *E*, *Triticum polonicum* (White Polish).

*Aegilops triuncialis* was pollinated with six varieties of common wheat (*Triticum vulgare*). These included both spring and winter, and red-grained and white-grained forms. Of 44 flowers pollinated by these six varieties, 27, or 61.4 per cent, produced seeds, from which 19 plants were grown. One or more seeds were produced in the case of each variety used.

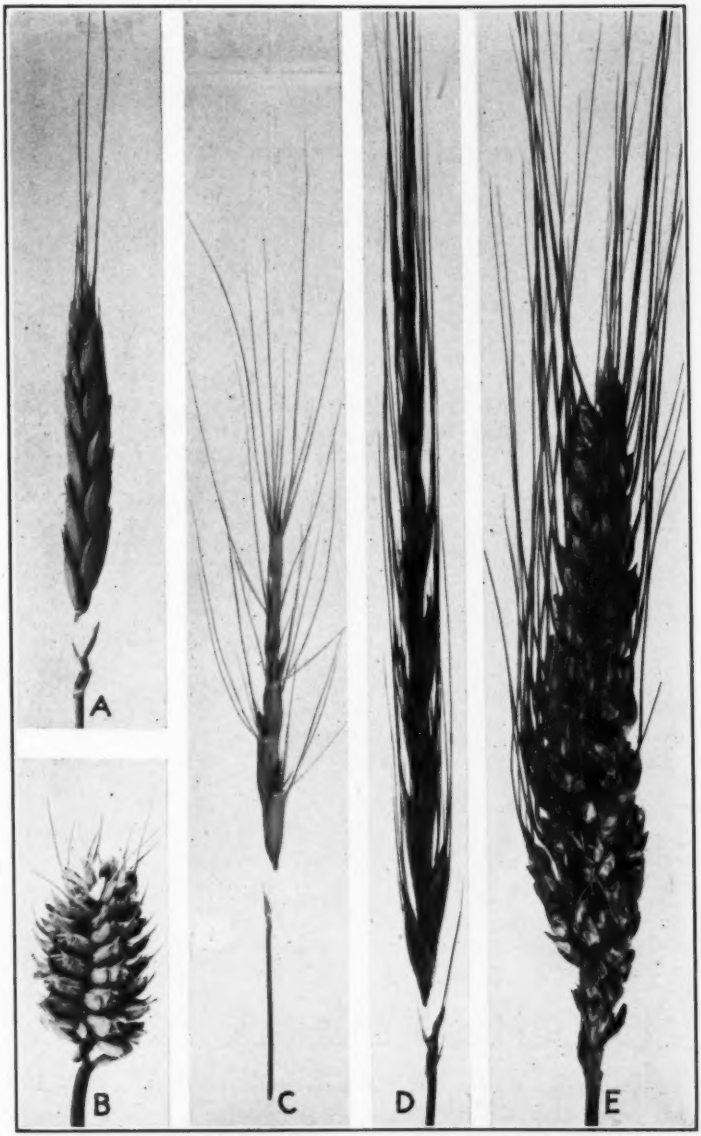


FIG. 12.—Spikes: *A*, $F_1$ of *Aegilops triuncialis* ♀ × *Triticum compactum* ♂; *B*, *Triticum compactum* (Dale Gloria); *C*, *Aegilops triuncialis*; *D*, *F*, of *Aegilops triuncialis* ♀ × *Triticum turgidum* ♂; *E*, *Triticum turgidum* (Alaska).

Pollen from *Aegilops triuncialis* was used on 62 flowers of three varieties of common wheat, 5 seeds being produced, a percentage of 8.1. The Walker variety did not produce seed. Only two plants

FIG. 13.—Spikes: *A*, *Aegilops triuncialis*; *B*, $F_1$ of *Aegilops triuncialis* ♀ × *Triticum spelta* ♂; *C*, *Triticum spelta* (White Bearded); *D*, $F_1$ of *Aegilops triuncialis* ♀ × *Triticum vulgare* ♂; *E*, *Triticum vulgare* (Purplestraw).

were produced from these seeds. An $F_1$ spike of the cross between *A. triuncialis* and the soft red winter variety Purplestraw, and spikes of the two parents, are shown in Figure 13. This cross produced vigorous $F_1$ plants but they were self-sterile.

### Summary of Aegilops-Triticum Crosses Made

Summarizing Table 1, it is found that 516 flowers on 109 spikes of *Aegilops ovata* pollinated by nine species of Triticum produced 230 seeds, or 44.6 per cent of successful pollinations. In the crosses with *A. ovata* the highest percentage, 73.3, was obtained when *T. turgidum* pollen was used; the second highest, 61.3, with *T. vulgare;* and the third highest, 56.3, with *T. compactum. T. durum, T. polonicum,* and *T. spelta* pollinations were each successful in about 40 per cent of the cases, while the percentages of successful pollinations with *T. dicoccum* and *T. dicoccoides* were 24.1 and 21.9, respectively. The lowest percentage of successful pollinations was with *T. monococcum,* in which cross only 13 per cent of the *A. ovata* flowers produced seed. On account of the limited numbers of flowers pollinated in most cases, and the more or less varying conditions under which such work usually must be done, there is perhaps little significance in the variation in percentages of successful pollinations when the different species were used.

When *Aegliops triuncialis* was used as the female parent, 134 flowers on 20 heads, pollinated by the same species of Triticum as used in the above crosses, produced 61 seeds, or a percentage of 45.5 of the total pollinations. In most cases few pollinations of *triuncialis* were made. The results obtained from *triuncialis* with the different species of wheat, therefore, are even less comparable than in the crosses with *A. ovata.* The percentages of the pollinations which were successful varied from about 80 per cent for both *T. compactum* and *T. durum* to 14.3 per cent for *T. turgidum.* In this latter case only 14 flowers were pollinated, and so it can not be concluded that this combination is essentially different from the others.

Reciprocal crosses in which wheat was used as the female parent were much less successful. From 161 flowers on 8 heads of the 3 Triticum species, *durum, compactum,* and *vulgare* pollinated by *Aegilops ovata,* only 5 seeds were obtained, or a percentage of 3.1. From 144 flowers on 9 heads of 4 Triticum species, *dicoccoides, durum, compactum,* and *vulgare,* pollinated by *A. triuncialis,* 15 seeds were obtained, or a percentage of 10.4. The poor results in these reciprocal crosses, in which wheat is used as the female parent, in contrast to its use as the pollen parent, are attributed partly to the fact that all the flowers of a single wheat head are not receptive at the time of the single pollination. It is likely, however, that some incompatibility between Aegilops and wheat exists in the case when wheat is used as the female parent that does not exist when Aegilops is so used, just as appears to be the case in wheat and rye when rye is used as the female parent.

It is evident from the data in Table 1 that, for the most part, the different species and varieties of wheat used cross readily with *Aegilops ovata* and *A. triuncialis* when the latter are used as the female parents. The largest number of crosses with any species of wheat were made with *vulgare,* in both cases. The percentages of success attained when *A. ovata* and *A. triuncialis* were pollinated with *T. vulgare* pollen were 61.25 and 61.36 per cent, respectively. In crosses made in the greenhouse the same year between different varieties of *vulgare* wheat, only 35 per cent of the pollinations made resulted in the production of seed. However, it should not be concluded that *A. ovata* and *A. triuncialis* are more compatible with

*T. vulgare* pollen than is the pollen of one variety of *T. vulgare* with another. Under favorable greenhouse conditions, *A. ovata*, usually having only three spikelets to the head, completes its blooming in two days and occasionally in one, while *A. triuncialis*, which has five or six spikelets, requires a slightly longer period. In wheat grown under similar conditions, however, the complete blooming of all flowers on a single head commonly requires a period of five or more days, although the removal of flowers and spikelets in preparation for pollination somewhat reduces this period for any head. All of the flowers that were used for crossing on a head of *A. ovata*, therefore, are receptive at about the same time, and all flowers pollinated on a head produced seed in several cases (Table 1). The larger number of spikelets of *A. triuncialis* utilized in crossing, however, may result in some of the flowers on a head not being receptive at the time of a single application of pollen. It is even more probable that some of the 18 to 24 flowers utilized for crossing in a head of *T. vulgare* would not be receptive at the time of a single pollination, especially under greenhouse conditions.

### Hybrids Between Secale Cereale and Aegilops Species

Crosses were made between rye (*Secale cereale*) and three species of Aegilops, viz, *ovata*, *triuncialis*, and *ventricosa*, rye being used as the pollen parent in all cases. The results of these crosses are given in Table 2. From 180 flowers of *ovata* crossed with rye, 51 malformed seeds were produced, a percentage of 28.3. Very few of these seeds germinated, and only two plants were matured. Spikes of the $F_1$ and of the parents are shown in Figure 14, and enlarged spikelets in Figure 15. The $F_1$ was completely sterile. The pubescent peduncle of rye was dominant in the $F_1$; spikelet characters are somewhat intermediate.

Table 2.—*List of hybridizations attempted and accomplished between Secale cereale and three species of Aegilops—ovata, triuncialis, and ventricosa*

| Hybrid combination and rye variety | C. I. No. | Number of heads worked | Number of flowers pollinated | Seed obtained | | Number of $F_1$ plants matured |
|---|---|---|---|---|---|---|
| | | | | Number | Per cent | |
| Aegilops ovata × Secale cereale: | | | | | | |
| Unknown | ---- | ---- | 180 | 51 | 28.3 | 2 |
| A. triuncialis × S. cereale: | | | | | | |
| Von Rümker | 133 | 1 | 6 | 0 | 0 | 0 |
| Rosen | 195 | 3 | 18 | 12 | 66.7 | 1 |
| Total | ---- | 4 | 24 | 12 | 50.0 | 1 |
| A. ventricosa × S. cereale: | | | | | | |
| Unknown | ---- | ---- | 54 | 28 | 51.9 | 0 |

Two varieties of rye were used in crosses with *Aegilops triuncialis*. The 24 flowers pollinated produced 12 seeds, a percentage of 50. From these seeds only one plant was obtained, of which a spike, together with those of parents, is shown in Figure 14. This plant was also completely sterile, and the pubescent peduncle of rye again was dominant. The spike of the *A. triuncialis* × rye hybrid is longer and more lax than that of *A. ovata* × rye, but in other respects they are similar.

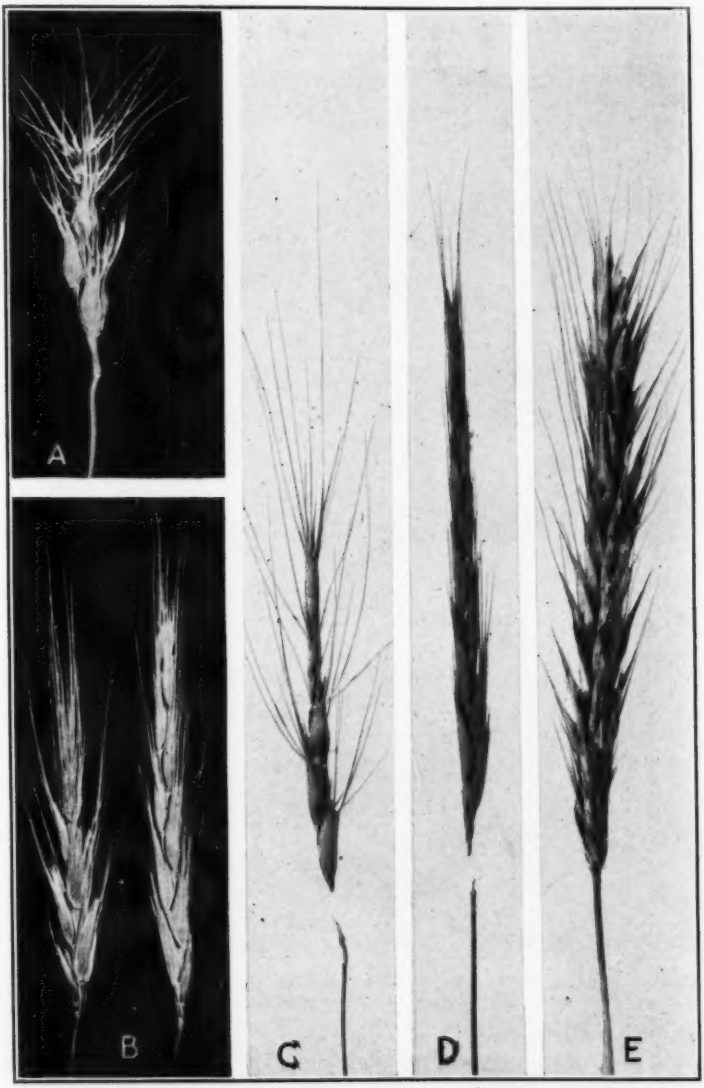


FIG. 14.—Spikes: *A*, *Aegilops ovata*; *B*, $F_1$ of *Aegilops ovata* ♀ × *Secale cereale* ♂; *C*, *Aegilops triuncialis*; *D*, $F_1$ of *Aegilops triuncialis* ♀ × *Secale cereale* ♂; *E*, *Secale cereale*

From 54 pollinations of *Aegilops ventricosa* with rye 28 seeds were obtained, none of which germinated.

Although 91 seeds were produced in these crosses between rye and Aegilops, and all were planted, only 3 plants have been grown. In all crosses involving Aegilops and rye, the seeds obtained were con-

FIG. 15.—Spikelets: *A, Aegilops ovata; B,* $F_1$ *of Aegilops ovata* ♀ × *Secale cereale* ♂; *C, Secale cereale*

siderably shrunken and lacking in endosperm development. These hybrid seeds germinated very poorly, and the few plants obtained were completely sterile. Hybrids between Secale and Aegilops have never been carried beyond the $F_1$ generation, so far as known to the present writers.

### Aegilops Ovata Pollinated With Barley

It is also of interest to note that from 141 pollinations of *Aegilops ovata* with cultivated barley, 26 kernels were obtained, all of which failed to germinate. These kernels likewise showed very poor endosperm development, and no embryos were observed. It appears that in these crosses of Aegilops with barley, and to some extent with rye, a limited endosperm growth has been stimulated by the pollen applied, but that this stimulation did not result in embryo formation. At least embryo development did not proceed very far, and endosperm development also soon ceased.

## THE $F_1$ GENERATION OF AEGILOPS-TRITICUM HYBRIDS

Two hundred and thirty-five seeds obtained from reciprocal crosses between *Aegilops ovata* and different species of Triticum, and 76 seeds obtained from reciprocal crosses between *A. triuncialis* and different species of Triticum, were sown in 6-inch pots in the greenhouse in December, 1922. Germination of the seed was poor, and there was a small additional loss after germination, the plants dying before the third leaf was produced. However, 97 plants matured from crosses between *A. ovata* and Triticum, and 49 from crosses between *A. triuncialis* and Triticum, this being 41.3 per cent and 64.5 per cent, respectively, of the seeds planted. All of the plants which matured proved to be true hybrids.

The $F_1$ plants matured in each of the following crosses consistently showed dwarfness and a reduced number of culms as compared with the normal $F_1$ plant of other crosses:

*Aegilops ovata* × Purplestraw (*Triticum vulgare*).
*Aegilops ovata* × Big Club and Dale Gloria (*Triticum compactum*).
*Aegilops ovata* × White Bearded spelt (*Triticum spelta*).

When the same wheats (with the exception of Big Club, which was not used) were crossed with *A. triuncialis*, the hybrids showed normal vigor. As great variability in vigor of growth is found in crosses between Aegilops and the several Triticum species used.

### Genetics of the $F_1$ Generation

Requien (*3, p. 788–789*) gave the name *Aegilops triticoides* to the plant occasionally found in the southern part of France, which later was shown to be the natural hybrid between Aegilops and wheat. Godron (*9*) applied this name to all $F_1$ hybrids between wheat and Aegilops. He did this because all of the $F_1$ Aegilops-wheat plants which he had observed were similar in appearance. Certain characters such as the shape of the head, form of the spikelets, spininess of the outer glumes, and sterility, were common to all his $F_1$ hybrids. He observed, however, that an awnless wheat used as a parent produced a hybrid with half-abortive awns, while an awned wheat resulted in a long-awned hybrid. Certain other differences observed were also ascribed to similar differences in the wheat parent. The hybrids of *A. ovata* × Triticum grown in connection with the present investigations closely resembled one another, differing only in such characters as were possessed by the wheat parent. For example, an awned wheat crossed with *A. ovata* gave a fully-awned $F_1$, while an awnless wheat when crossed with *A. ovata* produced a hybrid with the awns greatly reduced. The awns of the *A. ovata* × *T. durum* hybrid were longer than those of the *A. ovata* × *T. vulgare* hybrid, etc. The $F_1$ plants of *A. triuncialis* × wheat were distinguishable from

those of *A. ovata* × wheat principally by having a more slender head, more spikelets, and a smaller number of awns or teeth on the glumes. Otherwise the two groups of hybrids were similar and at times indistinguishable. The nature of the $F_1$ inheritance of 10 characters differentiating the Aegilops and Triticum parents is shown in Table 3.

TABLE 3.—*Nature of inheritance in the $F_1$ plant of characters differentiating the Aegilops and Triticum parents*

| Characters | Aegilops | $F_1$ | Triticum |
|---|---|---|---|
| 1. Sheath and leaves | Hairy | Intermediate | Few to none. |
| 2. Tillers | Many | Many | Few. |
| 3. Height of plant | Short | Intermediate | Tall. |
| 4. Culms | Bent | Semierect | Erect. |
| 5. Spikelets per head | Few | Intermediate | Many. |
| 6. Awns or beaks on the glume | 2–7 | 2–4 | 1. |
| 7. Glume | Spiny | Spiny | Smooth. |
| 8. Awns or teeth on lemma | 2–3 | 1–3 | 1. |
| 9. Glumes | Rounded | Keeled | Keeled. |
| 10. Disarticulation of head | Deciduous | Deciduous | Persistent. |

In Figures 3 to 13, inclusive, showing the heads of the parents and the $F_1$ plants, a general resemblance of the latter to the wheat parent may be observed. It is evident, however, from Table 3 and also from the various illustrations, that the Aegilops characters predominate in the $F_1$.

In crosses between wheat varieties, dominance usually occurs in the following spike characters: Awnlessness to beardedness, red glumes to white glumes, pubescent glumes to glabrous glumes, and club to fusiform shape of spike. With the exception of the last-named character, dominance was expressed in the Aegilops × Triticum crosses in the same manner as in crosses between wheat varieties. In the cross between varieties of wheat with clavate and fusiform spikes, the $F_1$ usually has a clavate or partially clavate spike. The *A. ovata* × *T. compactum* (Big Club and Dale Gloria) cross produced $F_1$ plants none of which showed any indication of clavateness (fig. 8). When *A. triuncialis* was crossed with Dale Gloria, however, the influence of the *T. compactum* parent was evident in the $F_1$, the spike being somewhat clavate in shape (fig. 12).

When *Aegilops ovata* and *A. triuncialis* were grown in the greenhouse, the number of culms produced was very variable, ranging in *ovata* from 10 to 90, with an average of 40; and in *triuncialis* from 10 to 70, with an average of 30. Common wheat (*Triticum vulgare*) grown under similar conditions in the greenhouse produced from 2 to 10 culms, with an average of 4. $F_1$ plants of the cross *ovata* × *vulgare*, grown under similar conditions, averaged 22.7 culms per plant, and $F_1$ plants of the cross *triuncialis* × *vulgare* averaged 33.

In height these same greenhouse-grown plants averaged about 18 inches in *Aegilops ovata* and 22 inches in *A. triuncialis*. The height of the wheat plants varied with the variety, averaging about 30 inches for some varieties of *T. compactum*, and about 42 inches for certain varieties of *T. vulgare*, *T. turgidum*, and *T. polonicum*, although some of these latter reached a height of about 60 inches. The $F_1$ *ovata* × *vulgare* plants averaged about 34 inches in height, and the $F_1$ *triuncialis* × *vulgare* about 37 inches. For the first-named cross the intermediate growth habit of the hybrid plant as compared with the parents is shown in Figure 16.

In number of awns produced the $F_1$ of the *Aegilops ovata* × *Triticum vulgare* cross is intermediate, as is evident in Figure 17. The *ovata* glume usually has four or five well-developed awns, while the glume of wheat has only a single awn or beak, which is often very short. The

FIG. 16.—Plants: *A*, *Triticum vulgare*; *B*, $F_1$ of *Aegilops ovata* ♀ × *Triticum vulgare* ♂; *C*, *Aegilops ovata*

$F_1$ of the cross illustrated has two long awns and several teeth. In the different hybrids there is considerable fluctuation in this character, but the $F_1$ is always rather definitely intermediate between the parents. The same condition exists in the $F_1$ of the cross between *A.*

*triuncialis* and common wheat, the glumes of which are shown in Figure 17. Here again the hybrid is rather definitely intermediate between the parents in development of awns.

FIG. 17.—Glumes: *A, Aegilops ovata; B,* $F_1$ *of Aegilops ovata* ♀ × *Triticum vulgare* ♂; *C, Triticum vulgare; D, Aegilops triuncialis; E,* $F_1$ *of Aegilops triuncialis* ♀ × *Triticum vulgare* ♂; *F, Triticum vulgare*

## FERTILITY OF THE HYBRID PLANTS

The $F_1$ generation of Aegilops × Triticum hybrids generally has been found sterile, though Godron (*9*), Groenland (*11*), and Tschermak (*32*) present indisputable evidence that complete sterility does

not always occur. Godron believed the $F_1$ fertile only when backcrossed with wheat, but Tschermak suggests the possibility that some of the seeds in his $F_1$ plants were due to selfing. As no precautions appear to have been taken by Tschermak to prevent cross-pollination, his opinion is based on the fact that $F_2$ individuals which resembled the $F_1$ plants were self-fertile when pollination was controlled.

The present writers have had under observation more than 160 $F_1$ plants of crosses herein recorded between Aegilops and Triticum, grown under the following conditions: 7 fall-sown under field conditions; about 90 fall-sown in 6-inch pots in ordinary greenhouses; and about 60 likewise fall-sown in 6-inch pots, but in a greenhouse where the "length of day" was extended to about 16 hours by means of electric illumination. The plants grown under the lengthened-day conditions developed poorly, and were much inferior to those grown in ordinary greenhouses and in the field.

The flowers of the $F_1$ Aegilops-Triticum plants opened normally, and the anthers were extruded as in wheat. At the time of blooming these plants were examined frequently for any indications of fertility. Since self-fertility obviously can occur only when the anthers dehisce, careful scrutiny was maintained for this phenomenon. As shown in Table 4, natural dehiscence of anthers was observed on 16 plants, 14 of which were growing in the ordinary greenhouse and 2 in the field. On no plant in the lighted greenhouse did dehiscence occur, possibly on account of the inferior development of the plants. On the plants where dehiscence occurred the phenomena varied. In no case did all of the anthers on a single plant, or even all on a single spike, dehisce. Sometimes dehiscence occurred only on primary spikes, sometimes only on secondary spikes, but occasionally on both primary and secondary spikes. With the exception of those which dehisced naturally, the anthers on all $F_1$ plants were more or less deficient in their proper function, and microscopic examination revealed but few, if any, pollen grains that were viable. All of the 16 plants on which anthers were observed to dehisce naturally, however, produced one or more seeds. In addition to these 16 plants there were 14 others belonging to the $F_1$ generation which produced seed naturally, but in which, on account of the limitations on observation, dehiscence was not observed. As shown in Table 4, these 30 plants of the two categories produced a total of 154 seeds. There is reason to believe that most, if not all, of these seeds were from self-pollination. Although natural crossing appears to occur but rarely in the greenhouses where these plants were grown, the seeds produced on plants setting seeds naturally, but in which dehiscence was not observed, may possibly have resulted from backcrossing, though this is considered improbable. Fortunately, the pollination of 7 of the 16 plants on which anthers were observed to dehisce was controlled by inclosing single heads in glassine bags or by isolation of individual plants in a greenhouse where no wheat or Aegilops was grown. As seeds were obtained under these conditions, there is no doubt that self-fertility may exist in the $F_1$ of Aegilops-Triticum hybrids, the so-called *A. triticoides*. Godron's (*9*) conclusion that *A. triticoides* is always self-sterile is not substantiated in these experiments, therefore, although self-sterility is by far the more common condition.

TABLE 4.—*Numbers of seed-producing (self-fertile) $F_1$ plants of several Aegilops-Triticum hybrids in which the anthers were and were not observed to dehisce, and number of seeds produced in each case*

| Hybrid combination, and parental wheat variety | Seed-producing plants in which dehiscence was observed | | Plants setting seed naturally, but in which dehiscence was not observed | |
|---|---|---|---|---|
| | Number of plants | Number of seeds produced | Number of plants | Number of seeds produced* |
| A. ovata × T. dicoccum: | | | | |
| (Khapli) | 1 | 1 | 0 | 0 |
| (Black Winter) | 3 | 6 | 1 | 11 |
| A. ovata × T. durum: | | | | |
| (Arnautka) | 1 | 12 | 0 | 0 |
| (Kubanka) | 1 | 1 | 0 | 0 |
| A. ovata × T. vulgare: | | | | |
| (Ladoga) | 1 | 6 | 0 | 0 |
| A. triuncialis × T. dicoccum: | | | | |
| (Khapli) | 2 | 6 | 1 | 5 |
| A. triuncialis × T. dicoccoides | 2 | 3 | 1 | 2 |
| A. triuncialis × T. durum: | | | | |
| (Peliss) | 0 | 0 | 4 | 30 |
| A. triuncialis × T. turgidum: | | | | |
| (Alaska) | 2 | 44 | 0 | 0 |
| A. triuncialis × T. compactum: | | | | |
| (Dale Gloria) | 2 | 7 | 2 | 5 |
| A. triuncialis × T. spelta: | | | | |
| (White Bearded) | 0 | 0 | 3 | 7 |
| A. triuncialis × T. vulgare: | | | | |
| (Canadian Red) | 0 | 0 | 1 | 2 |
| (Sonora) | 1 | 3 | 1 | 3 |

* It is possible that some of these seeds were due to backcrossing, but this is considered improbable.

The only hybrids between *Aegilops ovata* and Triticum which showed self-fertility were those involving two varieties each of *T. dicoccum* and *T. durum*, and one variety of *T. vulgare*. The total percentage of self-fertility was very low. The 40 $F_1$ plants of the *ovata-vulgare* cross alone bore at least 15,000 flowers, but only 6 seeds were produced from self-pollinations. On the other hand, self-fertile $F_1$ plants were produced when *A. triuncialis* was crossed with *T. dicoccum*, *T. dicoccoides*, *T. compactum*, *T. turgidum*, and *T. vulgare*, and probably with *T. durum* and *T. spelta*, although, as already explained, dehiscence of anthers was not actually observed in these two latter crosses. The 49 plants of *triuncialis* and Triticum parentage produced 117 seeds when pollen was not applied artificially, while under the same circumstances the 97 plants of *ovata* and Triticum parentage produced only 37 seeds. Of the 117 seeds produced in the *triuncialis* crosses, however, 30 were produced in one cross, involving 4 plants of which Peliss durum wheat was one parent, and 44 seeds were from 2 plants of *A. triuncialis-T. turgidum* parentage. But one plant of the cross *ovata* × Black Winter emmer produced 11 seeds, and one plant of the cross *ovata* × Arnautka durum produced 12. So, while there is some evidence of greater general compatibility between Triticum and *triuncialis* than between Triticum and *ovata*, it is not conclusive in nature.

### BACK CROSSES ON THE $F_1$

Numerous back crosses were made on the $F_1$ Aegilops-Triticum hybrids grown in 1923, pollen not only from the parental wheat species represented in the original cross, but also from other species being employed in many cases, as is shown in Table 5. Since no

selfed seeds had been obtained, and no anthers had been observed to dehisce on $F_1$ plants grown previous to 1923, the usual procedure of emasculation had been dispensed with in pollinating the $F_1$ with parental types. A few successful back crosses thus made in 1922 proved their hybrid origin by certain characters which they possessed. This method was again followed in 1923, and all artificial pollinations of the $F_1$ plants of that year, shown in Table 5, were made without emasculation. On account of the self-fertility, which first was exhibited in this year in certain plants, it may be that a few seeds listed in Table 5 as originating from back crosses with wheat or Aegilops species may actually have originated by selfing.

TABLE 5.—*Number of flowers pollinated and seeds set on $F_1$ plants grown in 1923 from crosses between Aegilops ovata, A. triuncialis, and different species of Triticum when back crossed with parental and other species*

| Hybrid combination | T. vulgare | | T. compactum | | T. spelta | | T. dicoccum | | T. dicoccoides | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Flowers pollinated | Seeds set | Flowers pollinated | Seeds set | Flowers pollinated | Seeds set | Flowers pollinated | Seeds set | Flowers pollinated | Seeds set |
| *A. ovata* × | | | | | | | | | | |
| *T. vulgare* | 1,137 | 17 | | | 93 | 0 | 86 | 0 | | |
| *T. spelta* | 214 | 12 | | | | | 16 | 0 | 16 | 0 |
| *T. dicoccum* | 136 | 2 | 18 | 0 | 16 | 0 | 94 | 0 | | |
| *T. turgidum* | 446 | 12 | | | 32 | 0 | 62 | 0 | 28 | 0 |
| *T. durum* | 286 | 20 | | | 26 | 2 | 60 | 5 | 16 | 0 |
| *T. polonicum* | 70 | 1 | | | | | 30 | 0 | | |
| *T. monococcum* | | | | | | | 14 | 0 | | |
| Total | 2,289 | 64 | 18 | 0 | 167 | 2 | 362 | 5 | 60 | 0 |
| *A. triuncialis* × | | | | | | | | | | |
| *T. vulgare* | 984 | 16 | | | 62 | 0 | 82 | 0 | 122 | 0 |
| *T. compactum* | | | 92 | 1 | 46 | 3 | | | | |
| *T. spelta* | 78 | 4 | | | 66 | 1 | | | | |
| *T. durum* | 296 | 16 | | | 76 | 4 | 34 | 3 | 32 | 2 |
| Total | 1,358 | 36 | 92 | 1 | 250 | 8 | 116 | 3 | 154 | 2 |

| Hybrid combination | T. turgidium | | T. durum | | T. monococcum | | A. ovata | | A. triuncialis | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Flowers pollinated | Seeds set | Flowers pollinated | Seeds set | Flowers pollinated | Seeds set | Flowers pollinated | Seeds set | Flowers pollinated | Seeds set |
| *A. ovata* × | | | | | | | | | | |
| *T. vulgare* | | | 50 | 0 | | | 142 | 1 | | |
| *T. spelta* | 18 | 1 | | | | | | | | |
| *T. dicoccum* | | | | | | | 42 | 0 | | |
| *T. turgidum* | | | | | | | 16 | 0 | | |
| *T. durum* | | | 72 | 1 | | | 14 | 1 | | |
| *T. monococcum* | | | 24 | 0 | 28 | 0 | | | | |
| Total | 18 | 1 | 146 | 1 | 28 | 0 | 214 | 2 | | |
| *A. triuncialis* × | | | | | | | | | | |
| *T. vulgare* | | | 18 | 0 | | | 20 | 0 | 124 | 0 |
| *T. compactum* | | | 44 | 1 | | | | | 46 | 0 |
| *T. spelta* | | | 40 | 3 | | | | | 90 | 0 |
| *T. durum* | | | 78 | 5 | | | | | | |
| Total | | | 180 | 9 | | | 20 | 0 | 260 | 0 |

The crosses in which self-fertility was observed appear in Table 4, and the back crosses made appear in Table 5. The $F_1$ plants of the hybrids between *Aegilops ovata* and different varieties of *Triticum vulgare* (Table 1) were self-sterile, with the exception of the one in

which Ladoga was used as the *vulgare* parent, but 1.5 per cent of the flowers back crossed with *vulgare* pollen produced seeds. Back crosses with *vulgare* pollen were performed on 1,137 flowers borne by 10 $F_1$ plants from 8 of the crosses with different wheat varieties listed in Table 1. None of these plants produced many kernels when thus back crossed, but most of them were fertile to a small degree, a total of 17 kernels being produced. When back crosses were made on these $F_1$ plants with pollen of the Aegilops parent, *A. ovata*, only one kernel was produced by the 142 flowers pollinated. The pollen of *T. spelta*, *T. dicoccum*, and *T. durum* when used on these $F_1$ *ovata* × *vulgare* plants did not result in the production of a single seed.

Back crossing with *Triticum vulgare* pollen also resulted in seed production in one or more plants of all of the remaining *ovata-Triticum* hybrids, except those in which *T. compactum* or *T. monococcum* was used, in which cases back crosses were not attempted. Back crosses with *T. turgidum* pollen resulted in seed production only in the *A. ovata* × *T. spelta* hybrid. Seed was produced in the *A. ovata* × *T. durum* hybrid when pollinated by *T. vulgare*, *T. spelta*, *T. dicoccum*, *T. durum*, and *A. ovata*. Other attempted back crosses on *A. ovata* × Triticum hybrids were without result. Since a complete series of back crosses was not attempted, and conditions affecting those made were not fully comparable, the relative fertility of different hybrids and the effectiveness of pollens from different sources is not definitely established.

Back crosses on the hybrids between *Aegilops triuncialis* and Triticum were partially effective in each case when *vulgare* pollen was used, seed being produced by the $F_1$ of the *triuncialis* crosses with *vulgare*, *spelta*, and *durum*. The *triuncialis* × *vulgare* hybrids produced seed from back crosses only when *vulgare* pollen was used and three plants of this hybrid were self-fertile. The *triuncialis* × *compactum* hybrids produced seed from back crosses with *compactum*, *spelta*, and *durum*. The *triuncialis* × *spelta* hybrids produced seed from back crosses with *vulgare*, *spelta*, and *durum*. The *triuncialis* × *durum* hybrids were the most generally responsive to back crossing, seed being produced from pollinations by *vulgare*, *spelta*, *dicoccum*, *dicoccoides*, and *durum*, the only species used in back crossing. Pollen of *triuncialis* was not effective in back crosses on hybrids of which it was one of the parents.

Of the 3,088 $F_1$ *Aegilops ovata* × Triticum flowers pollinated with wheat species, 73, or 2.4 per cent, set seed, while of the 2,150 $F_1$ *A. triuncialis* × Triticum flowers similarly pollinated, 59, or 2.7 per cent, set seed. The two groups of hybrids thus appear to be about equally responsive to back crossing.

The low degree of self-fertility exhibited by these hybrids, and the increased but still low seed production resulting from back crossing, just cited, are in marked contrast to the results obtained in the original crosses. When *ovata* and *triuncialis* were crossed with different species of wheat as pollen parents, about 45 per cent of the pollinations were successful. It is plainly evident that the success attained in the original cross is no index of the fertility in the $F_1$ generation.

In this connection it should be noted that $F_1$ hybrids involving both *Aegilops ovata* and *A. triuncialis*, of which durum wheat was one parent, were the most generally fertile of all the hybrid com-

binations studied, on back crossing with the different wheat species. The *A. ovata* × *Triticum durum* hybrid produced seed when back crossed with 4 different Triticum species and also with *ovata*, and the *triuncialis* × *durum* hybrid produced seed when back crossed with 5 different Triticum species. Self-fertility also was present in certain plants of each group of these *durum* hybrids.

The reason is not evident for this apparently greater compatibility between *Triticum durum* and the two species of Ageilops used than was found in hybrids with other species of Triticum. The chromosome number in *durum* is 14 (haploid), the same as in *ovata*, but *turgidum*, *dicoccum*, and *polonicum* also have 14 chromosomes, so the chromosome number does not appear to be the decisive factor. Backcrosses with wheats with 14 and 21 chromosomes also were about equally effective in seed production. The $F_1$ plants of these *durum* hybrids made a vigorous growth, but did not exceed certain other hybrids in this respect. It appears, then, that there is a relatively greater degree of compatibility between certain durum wheats and the species of Aegilops used, than between the other wheat species and these Aegilops species, for which no satisfactory explanation can be given.

## A STUDY OF THE SO-CALLED AEGILOPS SPELTAEFORMIS

The plants obtained as a result of back crossing the $F_1$ of Aegilops-Triticum hybrids with pollen of wheat sometimes have been known as *A. speltaeformis*. Jordan (*14*), who first proposed this name, believed that such plants formed a natural species.

The present hybridization studies have resulted in the production of many such plants, some of which already have matured. Data obtained on eight plants of this kind are given in Table 6 and spikes from three plants are shown in Figure 18. Seven of these plants were developed by back crossing the $F_1$ *Aegilops ovata* × *Triticum vulgare* hybrid with *T. vulgare* pollen, and one by similar back crossing with *T. spelta* pollen.

TABLE 6.—*Data on height, dehiscence of anthers, and number and percentage of seed produced on eight plants of Aegilops-Triticum parentage by selfing and by pollination with wheat*

| Parentage of plants | Height of plant | Anthers dehiscing | Number of flowers selfed | Seed set | | Number of flowers pollinated with wheat | Seed set | |
|---|---|---|---|---|---|---|---|---|
| | | | | Number | Per cent | | Number | Per cent |
| 1. (A. ovata × T. vulgare) × T. vulgare. | 36 | All | 262 | 1 | 0.38 | 22 | 1 | 4.55 |
| 2. Do. | 34 | All | 188 | 17 | 9.04 | 56 | 9 | 16.07 |
| 3. Do. | 30 | None | 222 | 0 | 0.00 | 168 | 9 | 5.36 |
| 4. Do. | 26 | Part | 200 | 0 | 0.00 | 30 | 5 | 16.67 |
| 5. Do. | 33 | Part | 125 | 1 | .8 | 40 | 0 | 0.00 |
| 6. Do. | 34 | All | 204 | 0 | 0.00 | 124 | 10 | 8.06 |
| 7 Do. | 30 | None | 94 | 0 | 0.00 | 72 | 1 | 1.39 |
| 8. (A. ovata × T. vulgare) × T. spelta. | 33 | Part | 90 | 3 | 3.33 | 142 | 43 | 30.28 |
| Total | | | 1,385 | 22 | | 654 | 78 | |
| Average | 32 | | | | 1.59 | | | 11.93 |

These plants varied in height from 26 to 36 inches, averaging 32 inches. The anthers dehisced fully in three of these plants, partly in three plants, and not at all in two plants. Four of the plants produced from 1 to 17 seeds by self-pollination, the percentage of self-

FIG. 18.—*A, B, C,* Spikes of the so-called *Aegilops spelta*eformis. (See text)

fertility varying from 0.8 to 9.04 per cent. Seven of the plants produced from 1 to 43 seeds when pollinated with wheat, the percentage of the flowers setting seed varying from 1.39 to 30.28 per cent of those pollinated.

These results are comparable to those of Fabre and Godron who obtained plants of the so-called *Aegilops speltaeformis* which apparently were self-fertile.

## SUMMARY

This paper reports the results of an extensive series of hybridizations of *Aegilops ovata* and *A. triuncialis* with *Triticum monococcum*, *T. dicoccum*, *T. dicoccoides*, *T. durum*, *T. polonicum*, *T. turgidum*, *T. compactum*, *T. spelta*, and *T. vulgare*, and also with *Secale cereale*. *A. ventricosa* also was used in a few cases.

Of the flowers of *Aegilops ovata* pollinated by Triticum, 44.6 per cent produced seed; and of *A. triuncialis* flowers so pollinated, 45.5 per cent produced seed. Reciprocal crosses resulted in 3.1 per cent of fertility with *A. ovata* pollen on Triticum species, and 10.4 per cent with *A. triuncialis* pollen. When *Secale cereale* pollen was used on *A. ovata* and *A. triuncialis* flowers the percentages of fertility were 28.3 per cent and 50 per cent, respectively. Seeds obtained in Aegilops-Secale crosses were poorly developed and germinated very poorly, and the plants obtained have been entirely sterile.

$F_1$ plants were matured from crosses between *Aegilops ovata* and one or more varieties of each species (or subspecies) of *Triticum* named, and also *Secale cereale;* the same is true for *A. triuncialis*, except in the cross with *T. monococcum*. Although there is a general resemblance of the $F_1$ plants to the Triticum parent, Aegilops characters predominate.

Self-fertility was shown to exist in the $F_1$ of Aegilops-Triticum hybrids, although self-sterility is by far the most common condition.

Numerous backcrosses were made on the $F_1$ plants, pollen from the parental and other species being used in many cases. Of the *Aegilops ovata*-Triticum flowers pollinated by Triticum species, 2.4 per cent produced seed; of the *A. triuncialis*-Triticum flowers, 2.7 per cent. Two seeds were produced in 214 $F_1$ *A. ovata*-Triticum flowers pollinated by *A. ovata* pollen. *A. ovata* and *A. triuncialis* pollen did not produce seed when used on $F_1$ *A. triuncialis*-Triticum flowers.

Hybrids in which *Triticum durum* was one parent were the most generally fertile on backcrossing, and were at least equally self-fertile in comparison with other hybrid combinations.

Plants obtained by backcrossing the $F_1$ of Aegilops-Triticum hybrids with pollen of wheat, often called *A. speltaeformis* by earlier writers, were partially self-fertile.

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# ANATOMY OF THE VEGETATIVE ORGANS OF THE SUGAR BEET [1]

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## INTRODUCTION

The first critical description of the structure of the sugar beet was published by van Tieghem (*15*).[2] He traced the ontogeny of the primary tissues and the mode of origin of the supernumerary cambiums and the endodermis, deriving both these tissues from the pericycle. Later investigators—de Bary (*1*), Morot (*7, p. 241*), Fron (*5*), and Strasburger (*14*)—mainly substantiated the work of van Tieghem.

As the early investigations were chiefly concerned with the origin and nature of the anomalous growth of the beet, they were naturally limited in their scope. An insight into the organization of the plant in its entirety was given by Droysen (*4*) and de Vries (*16*), and the work of the latter has remained a classic to the present day.

As the sugar beet gained in importance as an economic plant, a series of both technical and popular papers appeared dealing with certain features of the beet structure. The popular articles were largely by Briem (*2*), and were intended to give information to beet growers. Of the purely scientific papers, the account of Wiesner (*17*) deserves first mention. This contains an accurate description and classification of the different tissues of the beet, with special emphasis on the composition of the walls of the storage parenchyma. An understanding of the localization of the sugar in the different tissues was obtained through the researches of Peklo (*8*) and Colin and Grandsire (*3*).

Numerous attempts were made to correlate anatomical structure and sugar content, in the hope of arriving at better methods of selection in breeding for higher sugar content. The futility of these attempts is shown by the contradictory evidence obtained by Schindler (*11*), Briem (*2*), Schneider (*12*), Peklo (*8*), Geschwind (*6*), and numerous others.

Certain features of the anatomical structure have been critically reinvestigated in the last two decades. Through the work of Plaut (*9*), Rüggeberg (*10*), and Seeliger (*13*) there is now a correct understanding of the structure and distribution of the endodermis, the fate of the primary cortex, and the development of the primary and secondary tissues of the beet. The detailed and painstaking investigations of Seeliger have led to a modification of van Tieghem's concept of the origin of the supernumerary cambiums which had been taken over unreservedly by other investigators.

The object of the present paper is to give a compendium in the English language of the present knowledge of the structure of the

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[2] Reference is made by number (italic) to "Literature cited," p. 175.

sugar beet. The results of earlier investigations, carried on by different writers and at different times, were in need of testing; and further investigations were necessary in order that there might be obtained a picture of the inner organization of the beet which would be in harmony with present ideas. Comparative studies, so necessary for the proper evaluation of the normal anatomical picture, were limited to imperative requirements, but they will be extended by subsequent investigations.

## MATERIAL AND METHODS

The material was obtained partly from seedlings grown in the greenhouse, and partly from beets growing in the field in Colorado. The material was fixed with Flemming's medium solution and stained: (*a*) Delafield's haematoxylin and safranin, (*b*) Haidenhain's haematoxylin and safranin, (*c*) analine blue and safranin. Free-hand sections were examined in chloriodide of zinc or stained with phloroglucin and hydrochloric acid counterstained with chloriodide of zinc. Cork membranes were stained with Sudan glycerin.

All drawings are from photomicrographs, which were taken on Wratten M plates with B 58 and E 22 filters used singly and in combination.

## GROSS MORPHOLOGY

*Beta vulgaris L.* is a herbaceous dicotyledon, a member of the Chenopodiaceae. It normally completes its vegetative cycle in two years. During the first year it develops a large succulent taproot in which much reserve food is stored, and during the second year it produces flowers and fruits.

The mature beet is an elongated pear-shaped body composed morphologically of three regions—the crown, the neck, and the root. The crown is the broadened, somewhat cone-shaped apex. It bears a tuft of large succulent leaves and leaf bases. Adjoining it is the neck, a smooth narrow zone which is the broadest part of the beet and which constitutes ontogenetically the thickened hypocotyl. The root region, which forms by far the bulk of the beet tissues, is cone-shaped and terminates in a slender taproot. It is flattened on two sides, and often is more or less markedly grooved. The two depressions extend vertically downward or form a shallow spiral, and contain the lateral rootlets indistinctly arranged in two double rows. The surface of the beet is covered by a thin cork layer yellowish-white in color except on the aerial parts and at places of injury.

A well-formed beet has only one taproot. Occasionally the taproot branches and forms a number of thick stubby roots. The lateral roots are filiform, and originate from the two-arch xylem plate or from more peripheral rings of growth.

The leaves are arranged on the crown in a close spiral with the divergence of 5/13. The cotyledons, however, are arranged in opposite and decussating pairs. The lamina of the leaf is elongate triangular with rounded tip and undulate margin; the base is cordate and decurrent on the petiole, the latter being triangular in cross section and more or less flattened at the base. The venation is of the netted type. Lateral branches arise from a strongly developed midrib. These run obliquely outward, but before reaching the periphery they bend abruptly, run parallel with the surface, and

unite with the terminal ends of other lateral veins. The smaller veins anastomose freely, with the ultimate branches ending blindly in the parenchyma of the intercostal fields (fig. 1, A, B; fig. 10, B).

Unlike most cultivated plants, the beet shows a striking lack of uniformity in foliage characters. The most diverse types may be found growing side by side; plants with erect or flat foliage; short or long petioles, with lamina triangular or oblong; and straight or wavy margin and smooth or crinkly surfaces. There is also a great variation in the texture and thickness of the leaves as well as in the color, which may be either a dark green or a light olive, with numerous gradations between the two. When this paper was written investigations were underway with the object of isolating distinct foliage types in the hope of getting them sufficiently pure to breed true to form.

## ANATOMY

### STRUCTURE OF THE MATURE BEET

A median horizontal section through a mature beet shows a number of annular zones or rings of growth which are more or less equidistant, except near the periphery where they are very close together (fig. 2, A, B). Often, instead of a complete ring, smaller or larger segments of rings appear here and there; these are connected by their margin to the next inner ring. The center of the cross section is occupied by a two-lobed, more or less star-shaped core (fig. 3) from which radiate horizontal strands of vascular tissue—the root traces.

Each annular zone of growth is made up of a narrow ring of vascular tissue and a broad band of storage parenchyma. The ring of vascular tissue is composed of numerous collateral bundles separated from one another by medullary-ray tissue of varying width (fig. 4). In median longitudinal section the bundles of an individual ring are seen to anastomose tangentially, and between the bundles of successive rings there are obliquely descending radial connecting bundles. In the narrow tapering zone of the beet the number of annular rings decreases as the rings gradually unite with one another. A union of the rings is also effected in the apical leaf-bearing end, but here it is brought about by the passing out of the leaf traces. Each leaf is supplied with a number of traces of different degrees of development. The central trace extends horizontally through the complete radius of the cross section; the lateral traces do not extend so far, or they may even remain at the periphery. Owing to this arrangement, as pointed out by de Vries (*16*), the traces of one and the same leaf attach themselves to different annular rings, and, since they also tend to anastomose with one another, the relationship between all the leaves and the annular rings becomes very intimate.

The neck of the beet has, on the whole, root structure, except that in the upper region the central core opens up and incloses pith. As the neck passes into the crown this pith widens and frequently becomes hollow.

The composition of the vascular tissue is more or less alike for all bundles, with the exception of the central core and the peripheral region. The latter, however, differs only in that its bundles are immature, often represented only by undifferentiated cambium. The central core, on the other hand, exhibits a fundamental difference in that it contains both primary and secondary tissues. Its composition will be described in detail under development.

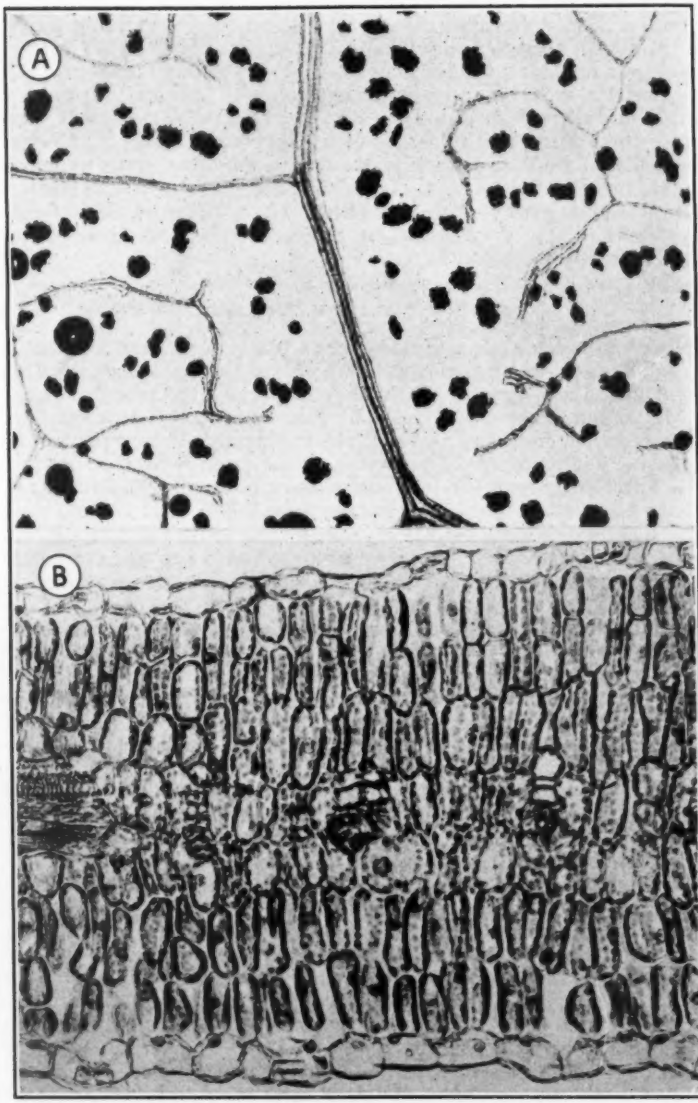


FIG. 1.—*A*. Part of beet leaf bleached to show venation. Note appearance of terminal veins ending blindly in the parenchyma. Dark spots are aggregates of calcium oxalate located in certain cells of the central mesophyll. × 66. *B*. Cross section through a thick leaf. Note that all of the mesophyll consists of palisade cells. × 272

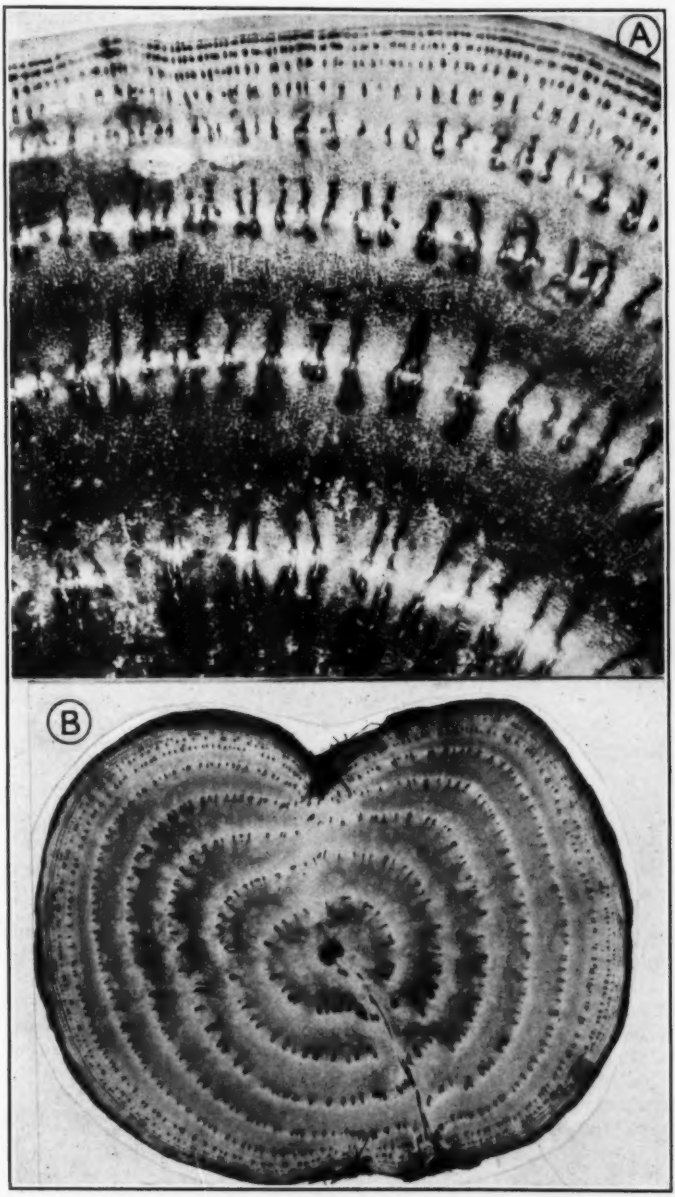


FIG. 2.—*A*. Partial cross section of a mature beet. × 4.75. *B*. Cross section of mature beet, natural size. Section treated with phloroglucin-hydrochloric acid to bring out the vascular bundles

The bundles of the mature rings are widest in the region of the cambium and taper gradually toward the phloem and xylem pole. This gives them the appearance of a double wedge.

The xylem is formed of a radial row of vessels with some lateral thick-walled tracheids and wood parenchyma (fig. 5, A, B). Fibers are found in only the oldest rings of the hypocotyl. The vessels are reticulate; the large ones are porous and have short articulations; the cross walls are strictly transverse but often sloping. The small vessels are more like tracheids, much pointed but porous. Typical tracheids are found only occasionally. The wood parenchyma is elongated and pointed, sometimes cross septate. The walls are perforated by numerous pits; the latter are round, sometimes lathyrate. The fibers, whenever they occur, are elongated and intertwine with their tips. In cross section the fibers are round or prismatic. The cells surrounding the xylem are thick walled and collenchymatous and lack intercellular spaces.

The phloem is composed of sieve tubes, companion cells, and phloem parenchyma (fig. 6, A, B; fig. 7, A). The sieve tubes have terminal as well as lateral sieve plates (fig. 7, B), which soon become covered with callus. The companion cells are of the same length as the sieve tubes, but sometimes they become cross septate. The phloem parenchyma cells are elongated and pointed, often also cross septate. There are numerous cells transitional to the typical storage parenchyma. The walls of the phloem parenchyma cells are strongly pitted, and the corners of all three types of phloem cells are more or less collenchymatously thickened.

The first-formed phloem groups of a bundle are seen as small obliterated areas recognizable only by their staining reaction. They occur commonly at some distance from the bundle due to enlargement and division in the phloem parenchyma.

Between the different bundles of a ring lies a narrow band of intermediate tissue, which, with reference to the bundle itself, is like a normal medullary ray. The parenchyma of these rays consists of radially elongated cells which undergo tangential divisions as the annular zones increase in diameter. Secondary medullary rays frequently develop inside the vascular bundles, causing a forking of the latter.

The concentric rings of vascular tissue are separated from one another by broad bands of storage parenchyma. The cells are large and almost spherical, the walls thin and extensively pitted. The outer and inner peripheries of this interzonal parenchyma contain vascular elements in addition; the outer periphery scattered xylem cells, the inner periphery obliterated phloem.

The lateral roots of the beet are very thin and are covered for a considerable distance with root hairs. The anatomical picture of root structure in these roots differs from that of the thickened taproot in a preponderance of xylem cells, especially vessels (fig. 8). Ray parenchyma is practically wanting. Often the primary xylem plate is triarch instead of diarch, as is always the case in the taproot.

### STRUCTURE OF THE LEAF

As seen in cross section, the vascular tissue of the petiole (fig. 9, A, B) forms a triangle which gradually widens basipetally. The number of bundles varies with the size and development of the leaf.

As the petiole merges into the midrib the number of bundles decreases, in that progressively more and more bundles fuse with one another. The large bundles of the petiole run separately from the base of the petiole to the insertion point of the lamina, while the smaller ones anastomose freely and form a network of wide meshes. The bundles are surrounded on all sides by cortical tissue which merges into col-

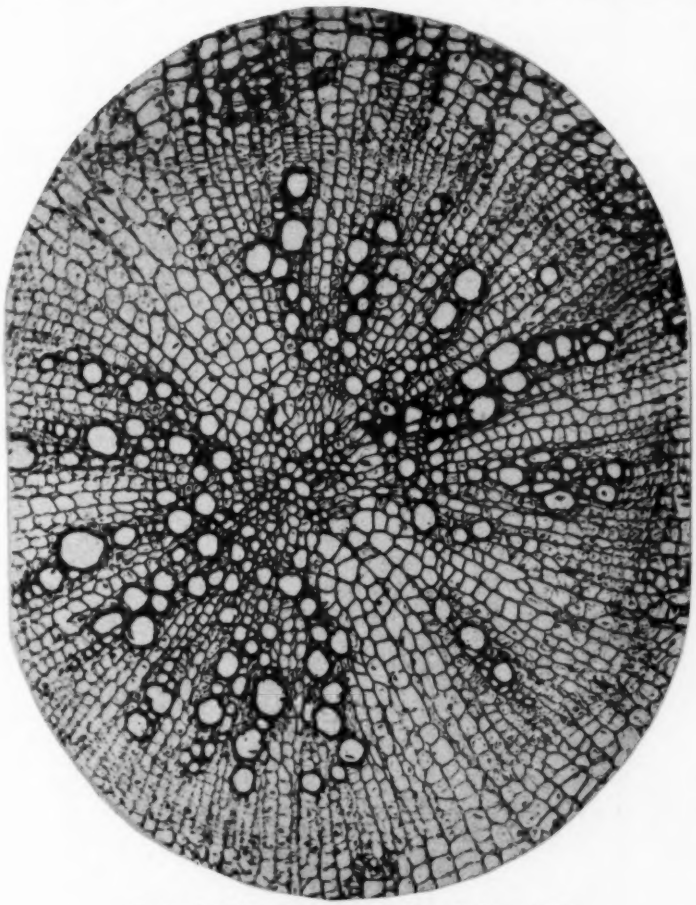

FIG. 3.—Central core of a young, actively growing beet. × 118

lenchyma just beneath the epidermis. The extent and distribution of the collenchyma can best be seen in Figure 9, A. This tissue forms a continuous band near the center of the abaxial surface and is otherwise limited to the projecting ridges. In the midrib it forms a continuous layer on both upper and lower surface.

The epidermis of the petiole is made up of elongated rectangular cells where it covers the collenchyma, and of somewhat elongated,

more or less polygonal, cells where it abuts directly on cortical parenchyma. The epidermis contains numerous stomates (fig. 10, A), except in the regions of collenchyma development. The cells of the

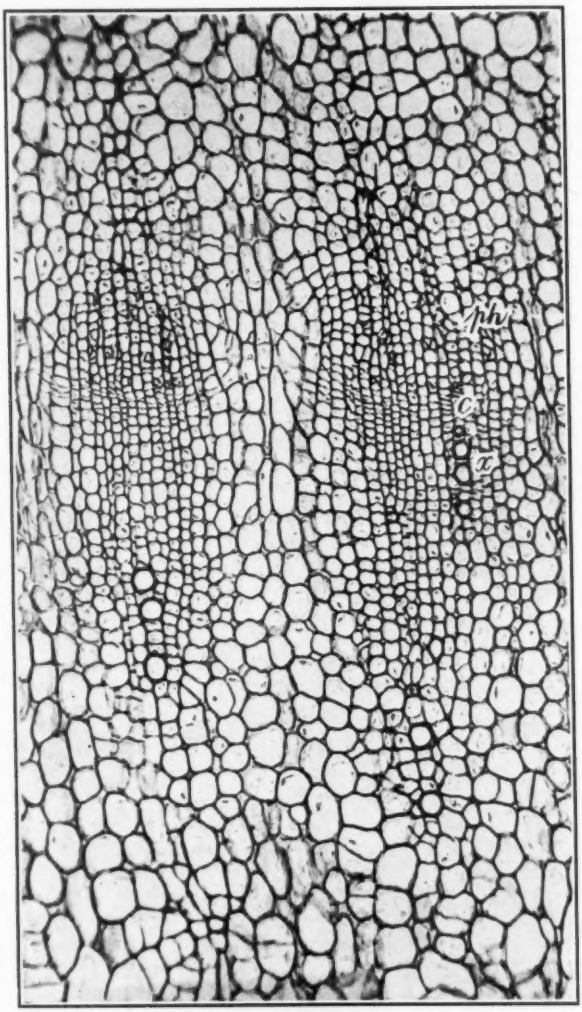


FIG. 4.—Vascular bundles from the outer zone of mature beet. *ph*, phloem; *c*, cambium; *x*, xylem, × 100

petiolar cortex are large, more or less barrel shaped, and are separated by large intercellular spaces. The peripheral cells contain chlorophyll; others, more or less scattered throughout the tissue of the petiole, contain crystal sand.

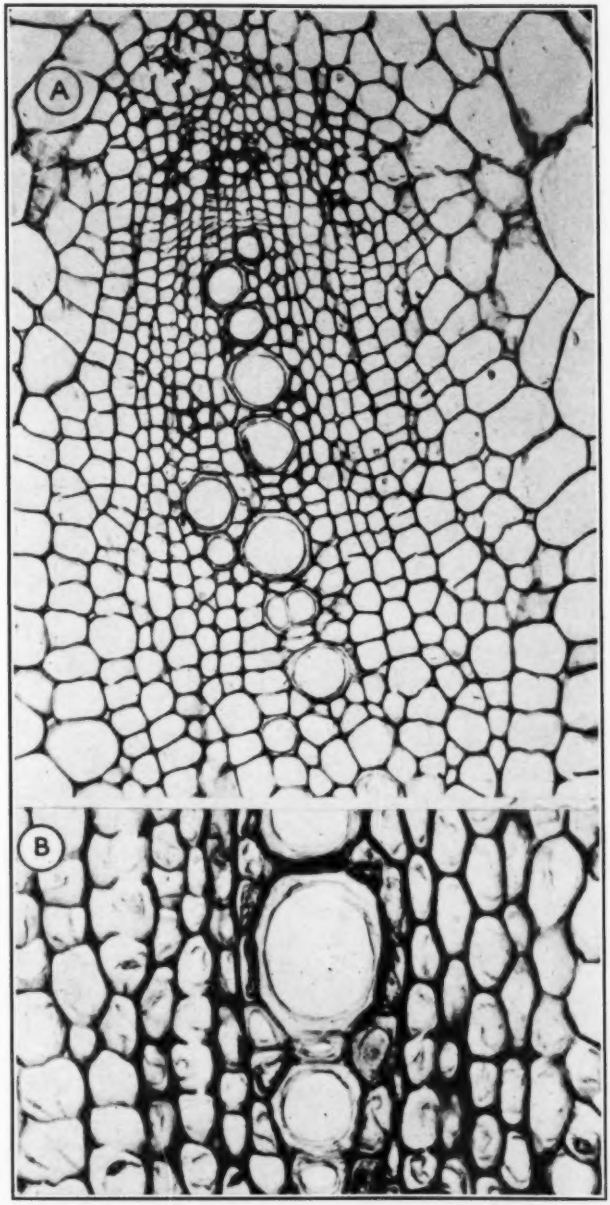


FIG. 5.—*A*. Typical bundle from mature beet. The sieve tubes show callus deposit and partial degeneration. × 170. *B*. Partial cross section of mature bundle. The parenchyma cells next to the xylem are thick walled and are spoken of as "sugar-sheath." × 500

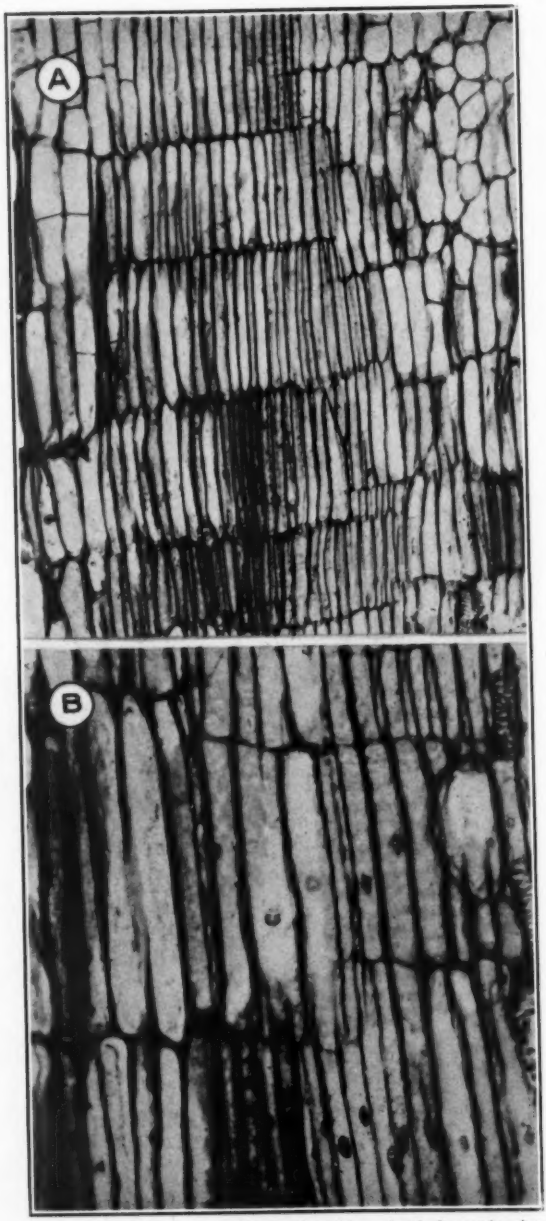


FIG. 6.—*A*. Radial section of phloem and cambium of actively growing ring. × 100. *B*. Radial section of phloem and cambium. × 260

The histological composition of the vascular tissue is that of typical collateral bundles. The phloem forms a narrow zone composed chiefly of sieve tubes with their companion cells and some phloem parenchyma. Above the phloem is a large sclerenchyma cap (fig. 11). A much less developed cap consisting of elongated thick-walled cells is found on the xylem pole of the bundle. Adjoining the latter is the protoxylem, interspersed with thin-walled fibers. The secondary wood forms a thick layer composed of numerous wide and narrow vessels and thick-walled fibers. Between xylem and phloem is the cambium formed of regular rectangular cells.

The epidermis of the lamina is unusual in being similar on both surfaces. The upper surface has irregular polygonal cells with tortuous walls (fig. 10, A). Toward the apex the cells become smaller. Here and there are small polygonal cells, the remains of young ephemeral hairs. In certain types of beets the mature leaves have very long, multicellular hairs, especially along the veins. Such leaves were sent to the writer from Rocky Ford, Colo., by A. W. Skuderna, who finds associated with this hairiness a high resistance to the leaf-spot disease. The cells of the lower epidermis are slightly more

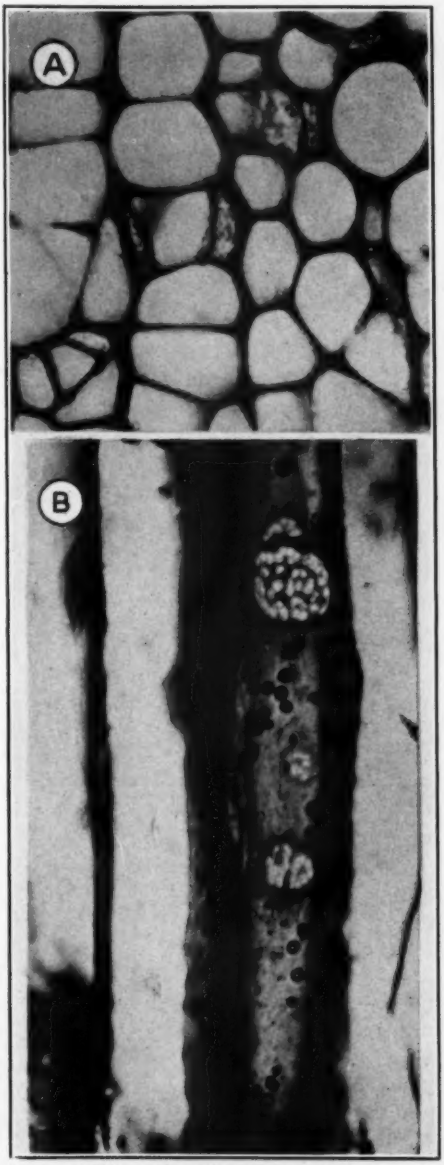


FIG. 7.—*A*. Mature phloem; the companion cells show granular content. × 1,000. *B*. Mature sieve tube with lateral sieve plates. × 1,000

irregular and the walls more tortuous. The stomates are of a simple type. The pores are surrounded by a pair of specialized guard cells which contain numerous chloroplasts. There are no accessory cells.

Stomates are found on both upper and lower surfaces (fig. 10, C), but are more numerous on the lower. De Vries (*16*) found on the upper surface an average of 91, and on the lower an average of 144

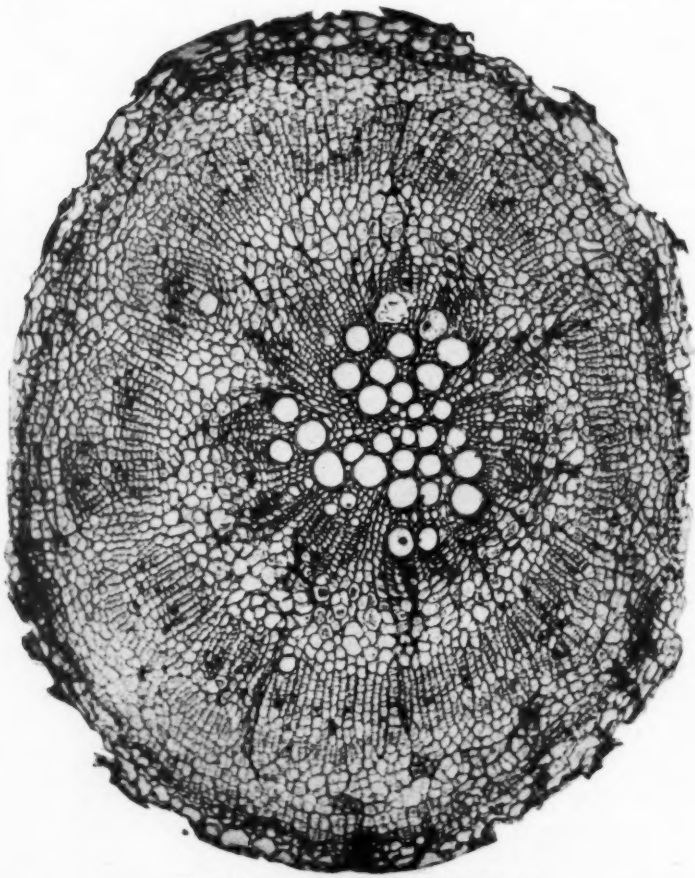

FIG. 8.—Cross section through tip of taproot. × 77

per square millimeter. Droysen (*4*) found 114 and 162, respectively.

In determining the number of stomates only the degree of maturity of a leaf appears to be a factor. The size of the leaf as well as the different local areas of the lamina—apex, base, margin, middle—play a lesser rôle. It was found that the regional distribution shows as great variation as the fluctuation within the local areas themselves. Young leaves have naturally the largest number of stomates; as many

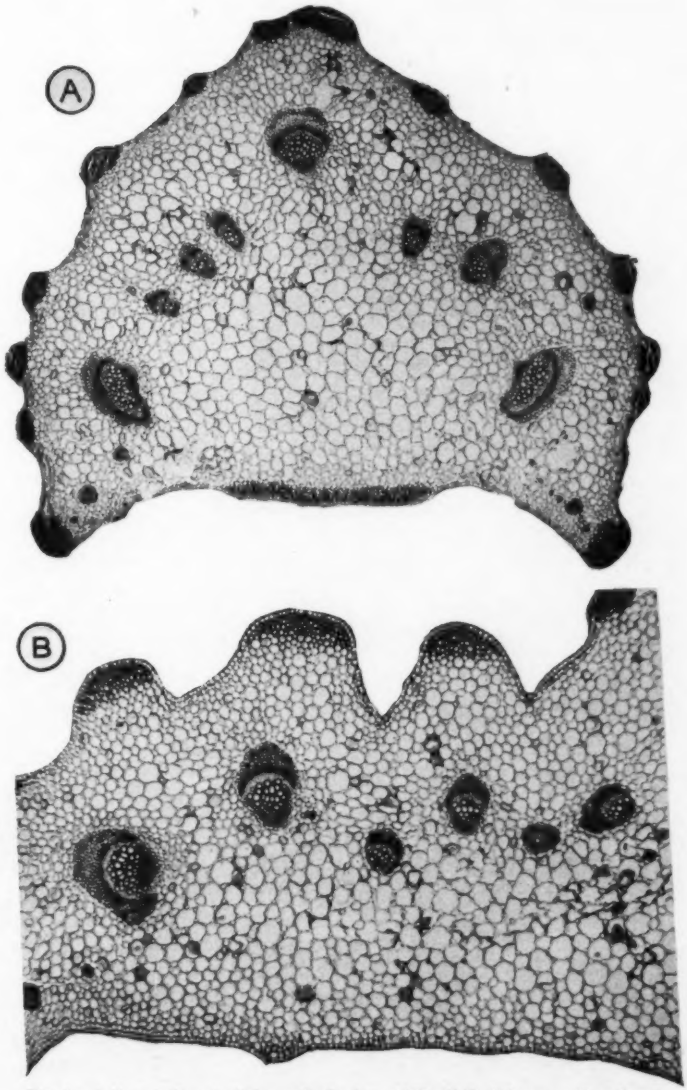


FIG. 9.—*A*. Cross section of petiole near the lamina. × 18. *B*. Partial cross section of basal petiole. × 28

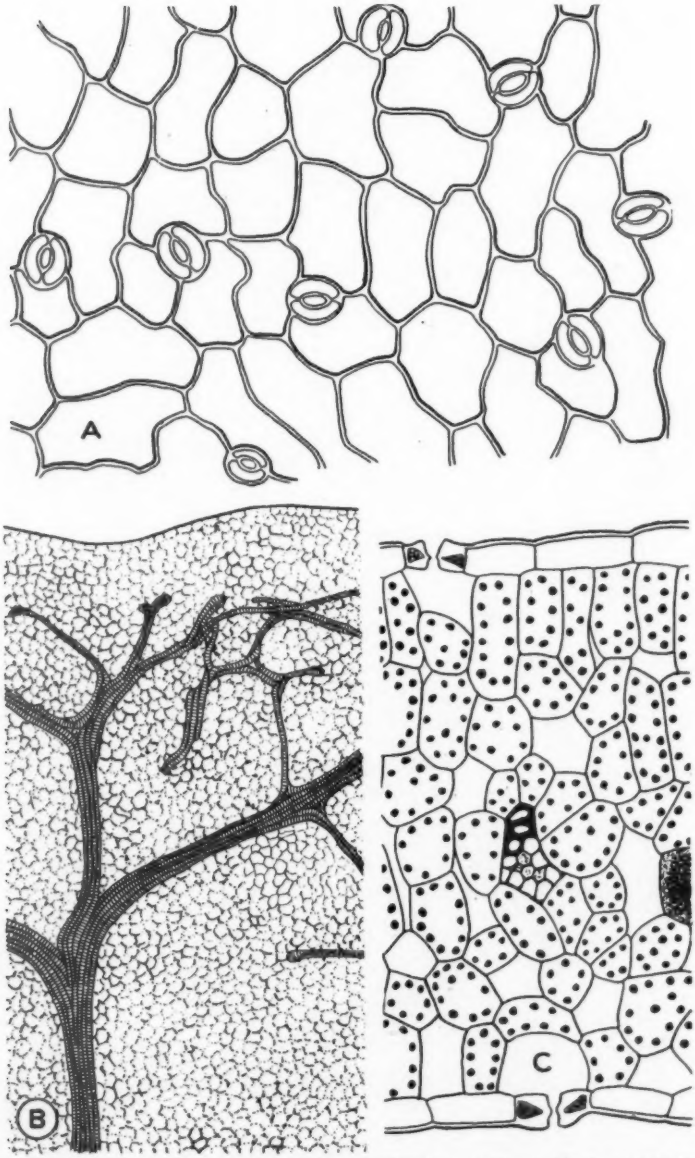


FIG. 10.—*A*. Upper epidermis, with stomates of mature leaf. × 296. *B*. Margin of leaf with terminal veins. × 90. *C*. Cross section of mature leaf [diagrammatic]. × 240

as 300 and more have been counted per square millimeter. These large counts are due to the fact that the epidermal cells are very small and that the stomates have not expanded to their full size. In seemingly fully developed, though still young leaves, the number

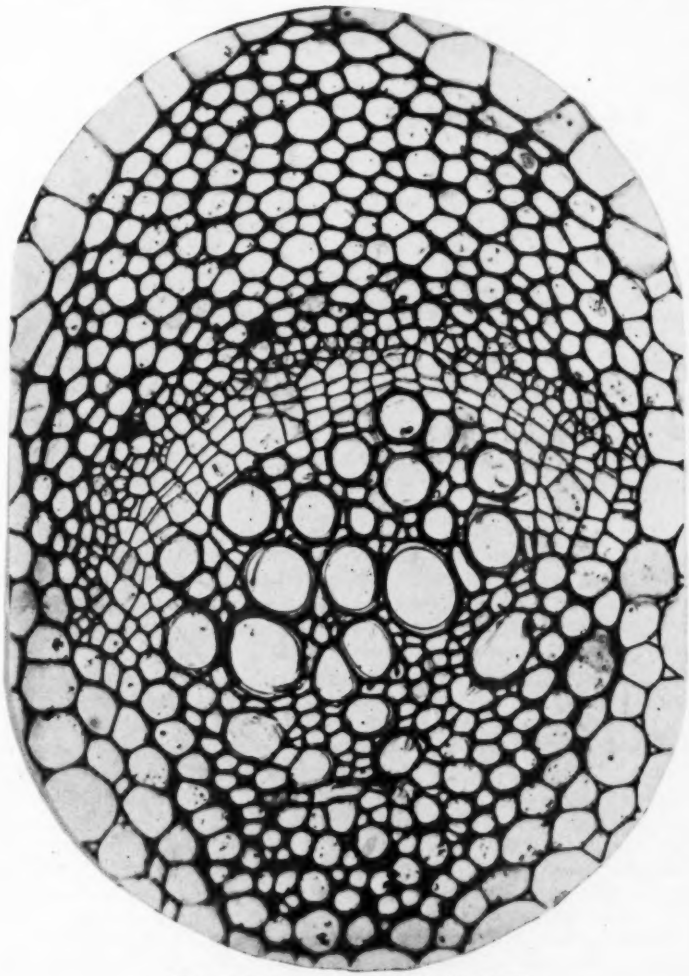

FIG. 11.—Cross section of petiolar bundle. × 303

is still often quite high, with a maximum count of 240 on the lower surface. In fully matured leaves the number is less, but shows a great deal of fluctuation in the different foliage types. Table 1 gives the number of stomates on upper and lower surfaces of leaves of different color, size, and thickness.

TABLE 1.—*Color, size, and thickness of leaves, and number of stomates*

| Color and size of leaf | Thickness of leaf | Number of stomates per square millimeter | |
|---|---|---|---|
| | | Upper surface | Lower surface |
| | *Mm.* | | |
| Light green; medium | 0.32 | 104 | 122 |
| Light green; large | .48 | 100 | 111 |
| Medium green; medium | .35 | 130 | 145 |
| Light green | .58 | 74 | 97 |
| Dark green; large | .48 | 75 | 90 |
| Dark green; very large | .56 | 60 | 59 |
| Dark green; medium | .28 | 73 | 79 |
| Medium green | .41 | 57 | 76 |
| Light green | .36 | 90 | 114 |
| Dark green | .45 | 76 | 119 |
| Light green | .41 | 77 | 99 |
| Light green | .40 | 138 | 167 |
| Dark green | .72 | 88 | 111 |
| Light green | .64 | 73 | 113 |
| Dark green | .36 | 103 | 116 |
| Dark green | .45 | 69 | 75 |

According to de Vries (*16*) and Droysen (*4*), the size of the stomates on the upper surface is 23 by 32 microns, while the size of those on the lower surface is a trifle smaller. Although these figures represent an acceptable mean, there is nevertheless quite a fluctuation in size in the different parts of a leaf and in different foliage types. Very old leaves have very large stomates, sometimes as long as 45 microns.

The mesophyll of the leaf is formed of parenchymatous tissue, the cells of which contain chloroplasts (fig. 10, C) and occasionally crystal sand. It is normally indistinctly divided into palisade tissue and spongy parenchyma. The palisade tissue is made up of small, more or less cylindrical cells; the cells of the spongy parenchyma are slightly larger and roundish in form.

The number of cell layers in a cross section of a leaf is practically constant, even though the thickness of the leaf varies greatly. In very thick leaves all cells are elongated into a uniform palisade tissue (fig. 1, B), whereas in very thin leaves typical palisade cells are altogether absent and the entire mesophyll consists of very short, roundish cells.

## ONTOGENY

Microscopically, the young seedling shows three regions: Root, hypocotyl, and cotyledons. The junction between hypocotyl and root is indicated by an abrupt tapering of the axis and the appearance of lateral rootlets. In very young seedlings this demarcation is less distinct. Seeliger (*13*) includes in the root the region from the root-cap to the piliferous zone, while the hypocotyl extends from the piliferous zone to the insertion point of the cotyledons.

The cotyledons are elongate elliptical, with the lamina narrowing at the base to form a short petiole. The anatomical structure is very simple. The tissue of the lamina is indistinctly divided into chlorophyll-bearing palisade cells and spongy parenchyma. The

latter contains numerous calcium oxalate cells. The epidermis is simple, and is composed of irregular polygonal cells with somewhat tortuous walls. There are numerous stomates distributed equally over the lower and upper surfaces. In the region of the petiole the epidermal cells become elongated, while the stomates become fewer and finally disappear. The conducting tissue is represented by fine collateral bundles which run longitudinally between spongy parenchyma and palisade tissue.

Both root and hypocotyl are terete. The center is occupied by a thin strand of primary vascular tissue, which is inclosed by a cortex and bounded at the periphery by a single-layered epidermis. The epirdermis in the apical root region is specialized, in that many of its cells are elongated to form hairs. The epidermis of the hypocotyl is cuticularized and, like the older root zone, is devoid of hairs.

The cortex is made up of three to seven rows of elongated barrel-shaped cells which are separated from one another by large intercellular spaces (fig. 12). The innermost layer of the cortex contains smaller and more regular cells; some of which contain crystal sand. Cortex and vascular tissues are separated by an endodermis. The cells composing this layer are four-sided and regular, and there are no intercellular spaces among them (fig. 12, D). The root tip, with the exception of the first few millimeters, has a primary endodermis which is characterized by the Casparian strips along the radial walls. Plaut (*9*) made a special study of the development of the endodermis of the sugar beet, and his findings were substantiated by this investigation. The primary endodermis extends axially over a distance of 3 centimeters, when it becomes secondary, which state is characterized by the development of a suberin lamella over the entire surface. The cells of the endodermis which lie opposite the protoxylem points pass into the secondary state later than the cells in the other regions. In the lower region of the hypocotyl the endodermis becomes primary again and finally disappears. In somewhat older seedlings, according to Rüggeberg (*10*), the primary endodermis extends within a few millimeters of the apex of the hypocotyl and assumes the secondary state as soon as the cortex no longer offers protection to the vascular tissue.

The central cylinder of root and lower hypocotyl is made up of a diarch protoxylem plate with alternating phloem groups, a single-layered pericycle, and a band of parenchyma between xylem and phloem (fig. 13). In the upper hypocotyl, however, phloem and xylem form collateral bundles while the center of the stele is occupied by a pith (fig. 14, B; fig. 18, B). The change in the arrangement of the vascular tissue which takes place in the upper hypocotyl is described in detail later.

The pericycle of the young stele forms a single-layered concentric ring next to the endodermis (fig. 13). Its cells are uniform in shape and more or less rectangular. Its embryonic progenitors are like the other parenchyma cells. Soon, however, they begin to divide and elongate axially. They remain small in cross section while the cells of the endodermis greatly enlarge.

Differentiation of the primary vascular tissue takes place close behind the growing region. Here the procambium forms a dense

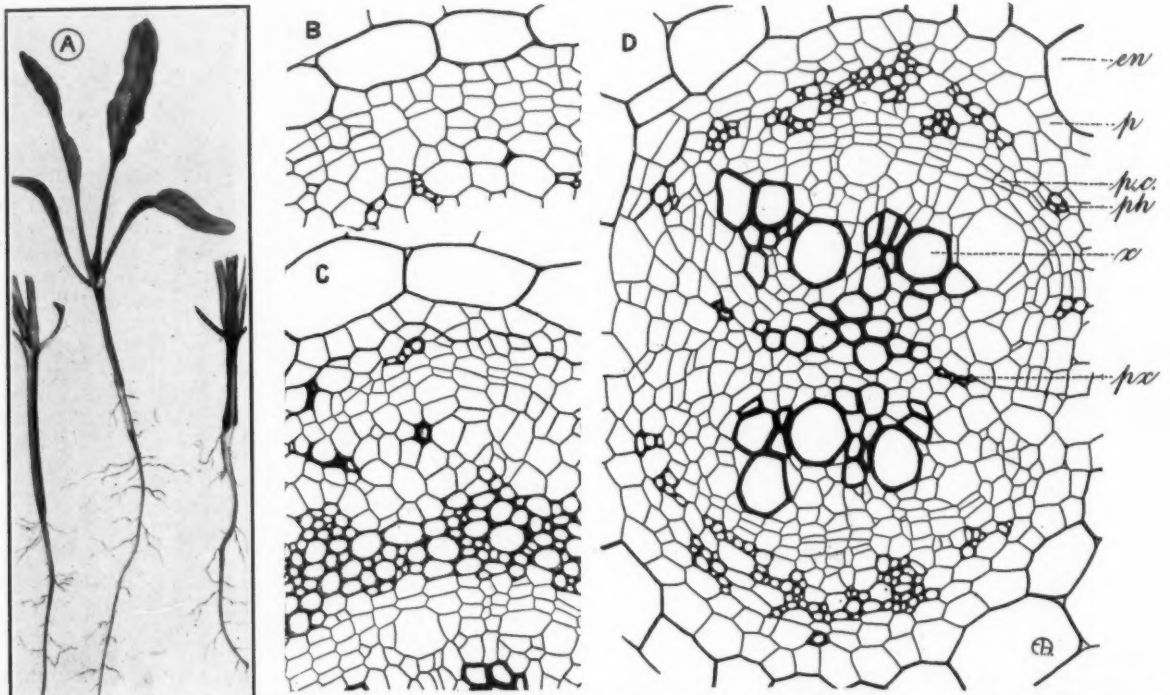


FIG. 12.—*A*. Beet seedlings about 15 days old. Seedling at the right shows the beginning of the sloughing off of the cortex. *B*. Development of a supernumerary cambium from cells of the pericycle. × 305. *C*. Development of a supernumerary cambium from the cells of the phloem parenchyma. × 305. *D*. Cross section through vascular tissue of young seedling. No supernumerary cambium has yet been formed. *en*, endodermis; *p*, pericycle; *p. c.*, primary cambium; *ph*, phloem; *x*, xylem; *px*, protoxylem. × 305

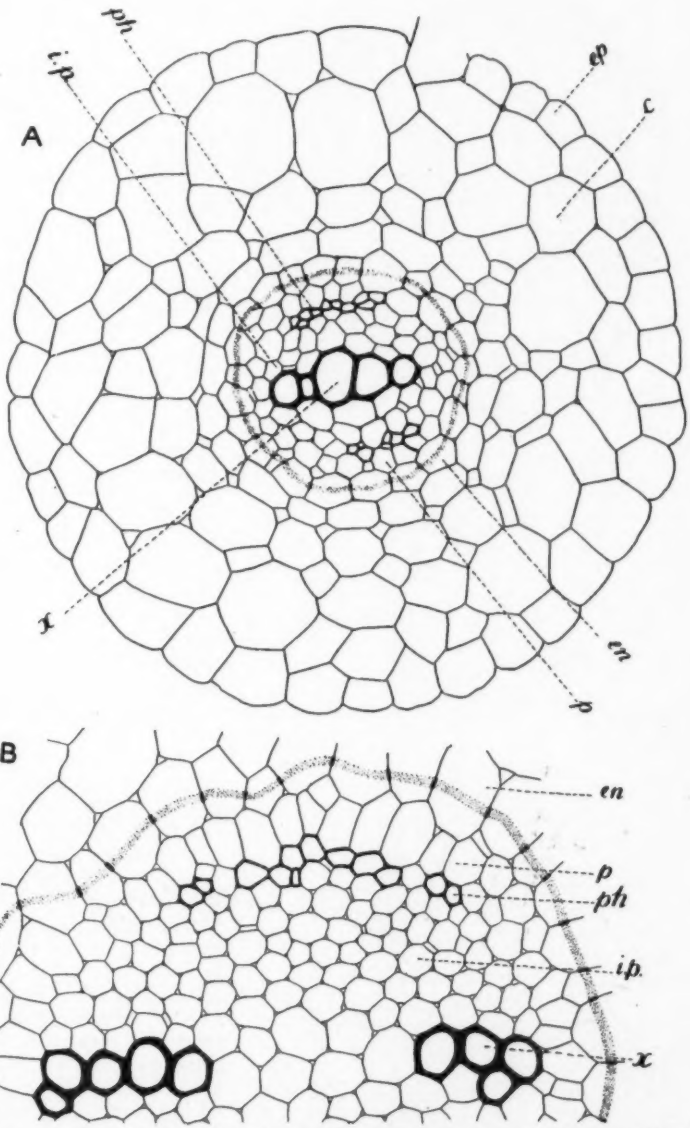


FIG. 13.—*A*. Cross section through young beet seedling. ×355. *c*, cortex; *ep*, epidermis; *en*, endodermis; *ph*, phloem; *i. p.*, interstitial parenchyma; *p*, pericycle; *x*, xylem. *B*. Partial cross section of young beet seedling. ×476. The interstitial parenchyma in which the primary cambium originates is much more developed here than in *A*

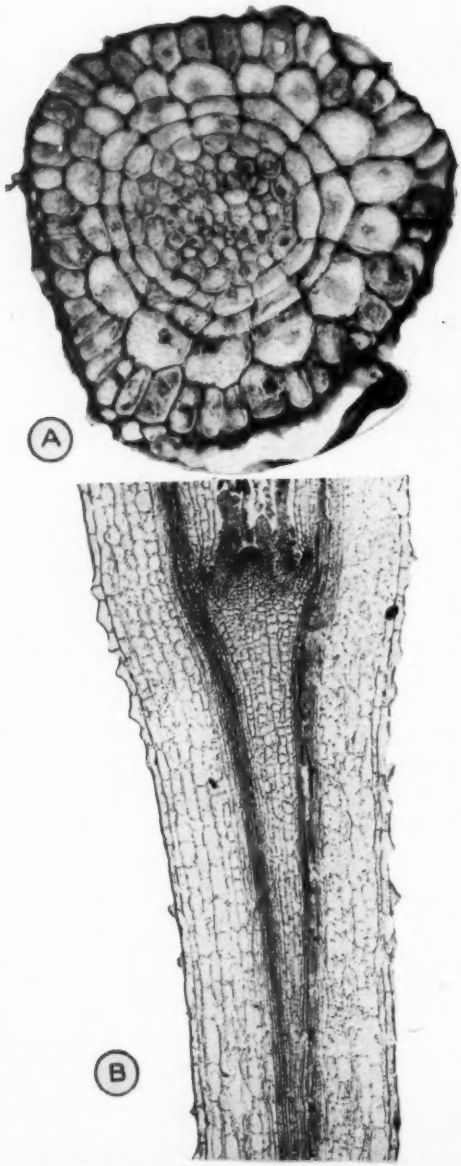


FIG. 14.—*A*. Cross section of young beet root. × 465. Note the formation of the first two sieve tubes of the vascular tissue. (See legend of Figure 15, *A*, for identification of issues.) *B*. Median longitudinal section of young seedling. × 46

tissue composed of elongated thin-walled cells. Specialization in these cells begins at a distance of about 2 millimeters from the calyptrogen. Two cells, lying adjacent to the pericycle and separated from one another by an angle of 180 degrees, have enlarged and divided to form the first sieve tubes and companion cells of the primary phloem (fig. 14, A; fig. 15). The sieve tube commonly abuts on the pericycle, but in the upper hypocotyl, according to Seeliger (*13*), the companion cell lies adjacent to the pericycle and the sieve tube next to it. Soon after the first phloem cells have differentiated, two other procambium cells which lie to the right and left of the sieve tubes undergo changes and mature into the first elements of the protoxylem. Differentiation in the protoxylem progresses centripetally until the two protoxylem points meet in the center to form the primary xylem plates. From now on xylem cells mature to the right and left of the xylem plate until all the cells of the primary wood have been formed (fig. 16). The first-formed xylem cells are narrow elongated elements with sloping or transverse end walls. They have secondary wall thickenings in the nature of rings or spirals. The later-formed cells are larger

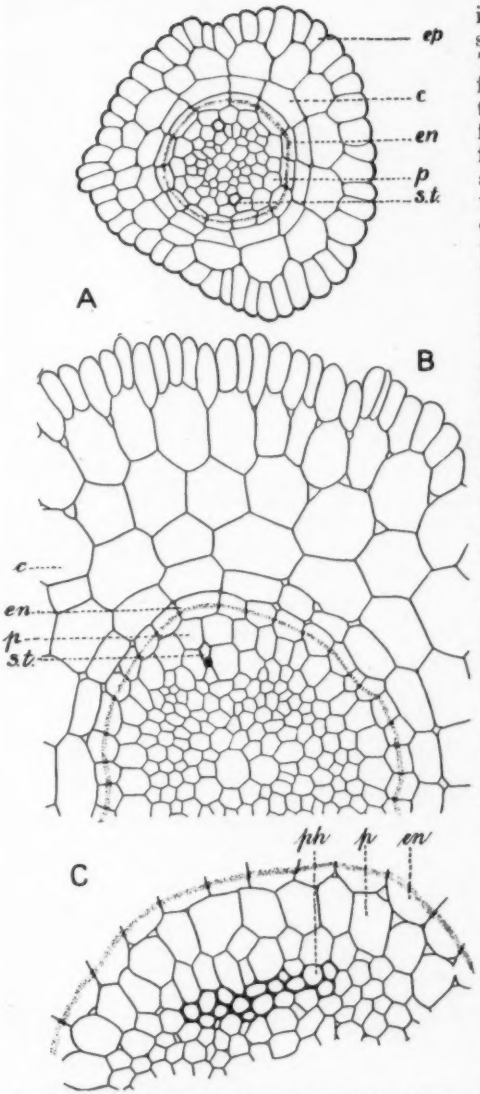


FIG. 15.—*A*. Cross section through young seedling root of beet. × 335. *ep*, epidermis; *c*, cortex; *en*, endodermis; *p*, pericycle; *s. t.*, sieve tube. Notice that the cortex is very narrow. *B*. Cross section through large seedling root of the same age. × 335. The first sieve tube and companion cell have differentiated, but no xylem. *C*. Cross section of a somewhat older root. × 580. Note the increase in the amount of phloem

in cross section but shorter longitudinally. They are reticulate or form transition stages to the spiral or ringed forms. The first-formed xylem elements are the protoxylem while the later-formed cells constitute the metaxylem of the primary wood.

Differentiation in the phloem is less readily followed, because of the small size of the elements. Seeliger (*13*) states that the metaphloem differentiates from procambium one or more cells to the inside of the pericycle. This later-formed phloem is made up of sieve tubes, companion cells and phloem parenchyma. In the region of the hypocotyl, xylem and phloem form collateral bundles in which the protoxylem is endarch. The change from the exarch condition in the root to the endarch condition in the upper hypocotyl is very abrupt, with the transition region extending over only a few millimeters. In this process, progressively differently situated procambium cells mature into vascular tissue. The two poles of the xylem plate, which in the root meet in the center, become separated, because of the failure of the procambium in this region to

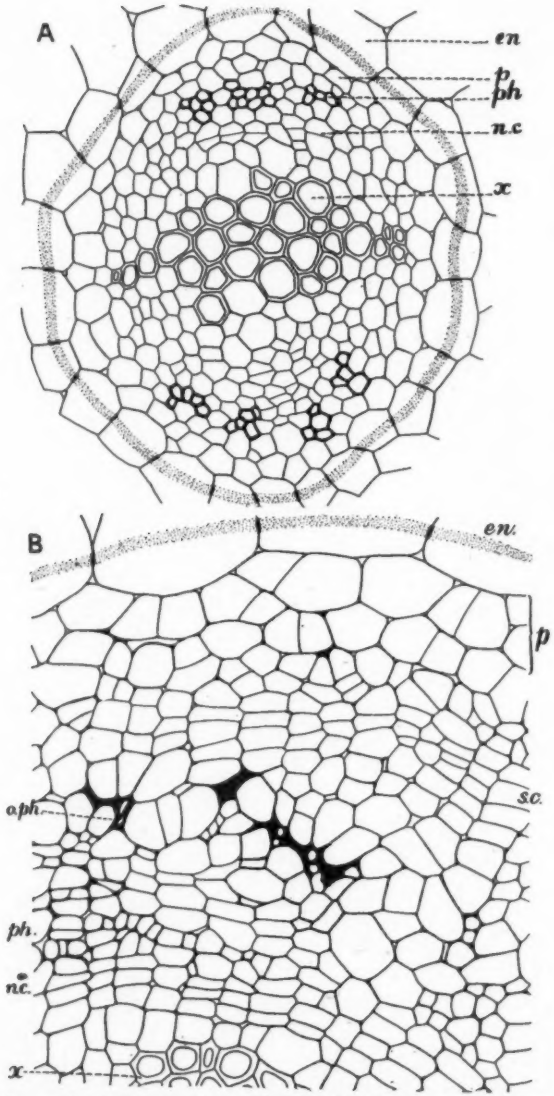


FIG. 16.—*A*. Cross section through young beet seedling root, showing development of primary xylem plate and the initiation of the primary cambium. *en*, endodermis; *p*, pericycle; *ph*, phloem; *n.c.*, normal primary cambium; *x*, xylem. × 373. *B*. Cross section through older seedling, showing development of the secondary cambium. *en*, endodermis; *p*, pericycle; *s.c.*, secondary cambium; *o.ph.*, obliterated protophloem; *ph*, phloem; *n.c.*, normal primary cambium; *x*, xylem. × 373

mature into xylem elements. Xylem differentiation becomes instead more prominent on either side of the two strands whereby the latter change their shape at first to triangular (fig. 17) and then to oval. Later-formed elements appear more and more to the inside until in the upper region of the hypocotyl the change from the exarch to the endarch arrangement has been completed. The phloem is also affected in this change from root to stem structure. The two phloem groups become divided, each forming two strands. Then two and two halves of opposite groups approach each other and come to lie external to the xylem with which they now form collateral bundles. While the central cylinder increases in size the cells of the cortex

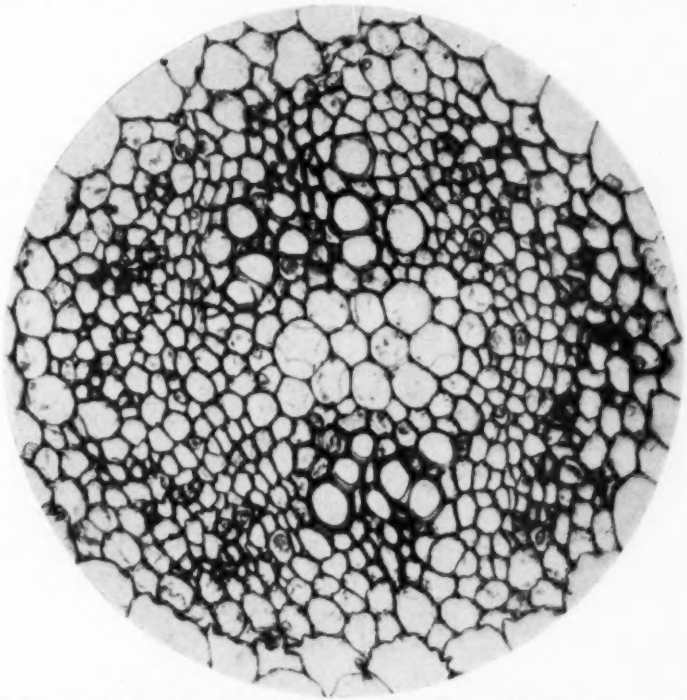

FIG. 17.—Cross section through hypocotyl of beet seedling. The xylem is changing from the exarch to the endarch condition. × 435

grow but little. They are at first passively stretched but later rupture and collapse. These changes are externally visible by the appearance of fine fissures which gradually widen, and finally the cortex is sloughed off.

This process takes place earlier in the root region than in the hypocotyl. In the latter the changes in the cortex due to radial expansion of the stele cause first an extension of the endodermis from the lower hypocotyl to the immediate vicinity of the growing region of the crown. Concomitant with the sloughing off of the cortex is the development of a periderm, which takes over the protective function of the primary cortex. Since the protoxylem is

formed in a region where there is much change and enlargement in radial and tangential directions, the elongation of the surrounding tissue causes the rings of the elements to be pulled farther apart, and, as the stretching continues, the cells may be flattened until the lumen is closed. Metaxylem and wood-parenchyma remain unchanged, but, according to Seeliger (*13*), suffer displacement due to radial contraction of the root, which takes place simultaneously with the development of the secondary tissues.

### SECONDARY GROWTH

The primary growth of the beet is concluded with the appearance of the second pair of leaflets; this normally takes from 10 to 12 days after the seed is planted. The largest diameter of the beet at that stage is at most only a few millimeters, while that of the mature beet is 15 centimeters or more. This increase in thickness is the result of cambial growth accompanied by independent cell division and cell enlargement of the parenchyma.

Cambial activity embraces two distinct phases: Differentiation and growth of the primary cambium and development of secondary cambiums. The primary cambium forms the innermost annular zone in the beet, while the secondary cambiums form a large number of supernumerary rings, of which, however, only the inner five or six mature their tissues. Since the origin of the primary and secondary cambiums differ, their development will be studied separately.

#### Development of the Primary Cambium

In the following description, unless stated differently, the anatomical picture is that of the lower hypocotyl or upper root region. Since growth and maturation of the tissues takes place acropetally, sections lower down will give younger developmental stages, those higher up more advanced ones.

When a seedling is about 10 days old and the second pair of leaflets becomes visible (fig. 12, A), the parenchyma cells between the primary xylem and phloem begin to elongate axially and undergo tangential division. A new meristematic zone thus arises which becomes the primary cambium and as such develops xylem and phloem in the normal manner. This cambium appears at first in the region of the two phloem poles, but gradually extends laterally over the two protoxylem points. In the latter case, however, the divisions which give rise to the cambium take place in the pericycle.

The xylem formed by the cambium unites intimately with the metaxylem of the primary wood (fig. 18, A). Occasionally, according to de Bary (*1*), a layer of parenchyma is interpolated between primary and secondary xylem. The zone in front of the protoxylem points remains free from secondary xylem; here the cambium forms parenchyma tissue which forms the two primary medullary rays.

Simultaneously with the formation of secondary xylem, the cambium is forming phloem centrifugally. This secondary phloem, like the xylem, becomes continuous with the primary tissue and indistinguishable from it (fig. 12, D). While the secondary phloem is forming, the primary phloem parenchyma enlarges and divides, thereby forcing the groups of sieve tubes apart; and since the latter have ceased development, they are at first stretched and finally obliterated

(fig. 12, C). The primary cambium continues active growth, but its office is soon to be yielded to another meristematic layer—the secondary or supernumerary cambium.

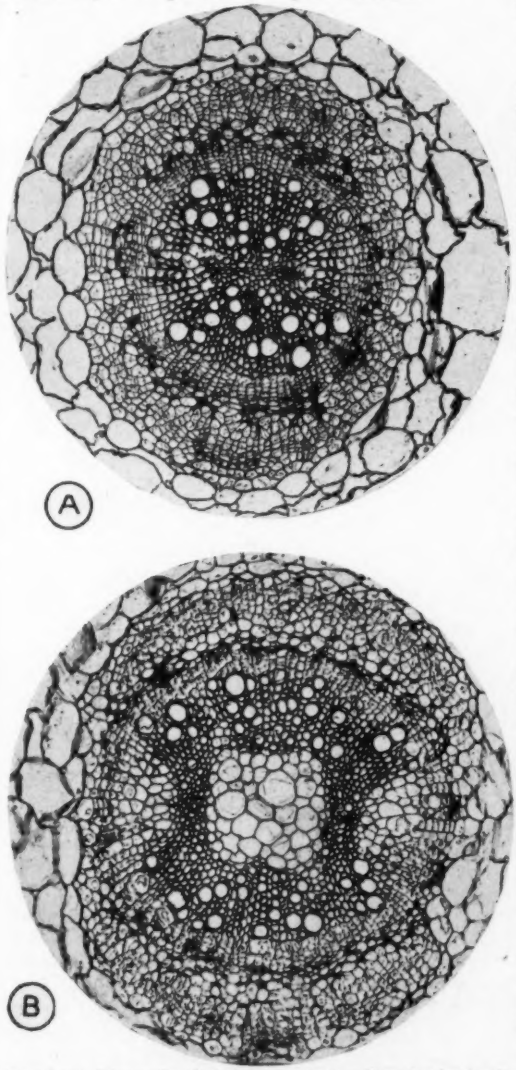


FIG. 18.—*A*. Cross section through a young beet seedling, showing development and activity of the primary and secondary cambiums. × 85. (See legend of Figure 16, *B*, for identification of tissues.) *B*. Cross section through the upper hypocotyl of the same seedling. × 85

### DEVELOPMENT OF THE SECONDARY CAMBIUM

The origin of the secondary cambium is not uniform for different regions of the beet, and even similar regions show pronounced deviations. The situation is perhaps best portrayed by the following remark of Seeliger (*13*) in the summary of his detailed ontogenetic studies: "In the development of supernumerary tissues it is not the morphological origin of a cell but its topographic relation to the axis and the neighboring tissues which determines its future."

In the early development of the seedling the first phloem cells develop adjacent to the pericycle, and the later developed metaphloem is separated from the pericycle by a single layer of undifferentiated procambial tissue. The cells of this layer enlarge and subsequently divide, thereby interpolating an ever-widening band of parenchyma between pericycle and phloem (fig. 15, B). This band of

parenchyma is not of uniform width, partly because cell division in the primary phloem parenchyma causes certain of the phloem groups to remain close to the pericycle. Seeliger does not mention this mode of development, but derives all this tissue from divisions in the phloem parenchyma. Soon there appear periclinal division walls in certain cells of this band, initiating the development of a secondary cambium. In the region of the protoxylem points, of course, the secondary cambium originates just as does the primary one in the pericycle (fig. 12, B).

This mode of development is characteristic for the root and the lower hypocotyl. In the upper hypocotyl the cambium arises altogether in the pericycle, while the central hypocotyl shows transition stages with more and more pericycle cells taking part in cambium formation as the apical region is approached.

Once initiated the cambium will produce an annular zone of bundles and parenchyma tissue. Since, however, additional cambiums are formed, the behavior of the first cambium initial differs from the normal behavior of cambium cells. When the cambium initial undergoes the first division, the outer of the two daughter cells becomes the initial of a new supernumerary cambium, while the inner daughter cell divides further and produces xylem, phloem, and medullary ray tissue. This process is repeated until all supernumerary cambiums have been formed. However there is no uniform method governing the formation of the supernumerary cambiums. Often sections of two supernumerary cambiums originate simultaneously, one from an inner, the other from a more peripheral phloem parenchyma cell. Since most of the supernumerary cambiums of the beet are initiated in quick succession, a beet no thicker than a pencil contains practically all annular zones of growth developing simultaneously.

### Periderm Development

The periderm of the beet always develops from cells of the pericycle. Its formation is initiated when the seedling has about five pairs of leaves, that is, at a time when the supernumerary cambiums are forming and the primary cortex is being sloughed off, and since this process takes place first in the root zone, the periderm develops acropetally, extending gradually into the hypocotyl. Periderm development begins with a conversion of the cells of the pericycle, by tangential divisions, into a band of meristematic tissue, which constitutes the phellogen or cork cambium. From the phellogen are formed, by reciprocal division, cork cells outside and phelloderm cells inside. The number of phelloderm cells, however, is smaller than the number of cork cells, since the latter are constantly being sloughed off and must be replaced. On the whole the periderm forms a thin covering from five to eight cells wide (fig. 19). The individual cork cells have the form of a parallelepiped with a five or six sided base. The height is less than the diameter of the bases, thus giving the cells a flattened appearance. The walls of the periderm cells are thin and suberized, except the middle lamella which is lignified.

### Development and Growth of the Annual Rings

As previously stated, the peculiar zonation noticed in a cross section of a beet is produced by concentric rings of vascular tissue inclosing broad bands of parenchyma. Near the periphery, however,

the rings are very narrow and the tissues just in the process of differentiation (fig. 20). By examining the different rings in centripetal order, one can easily follow out the ontogeny of a ring.

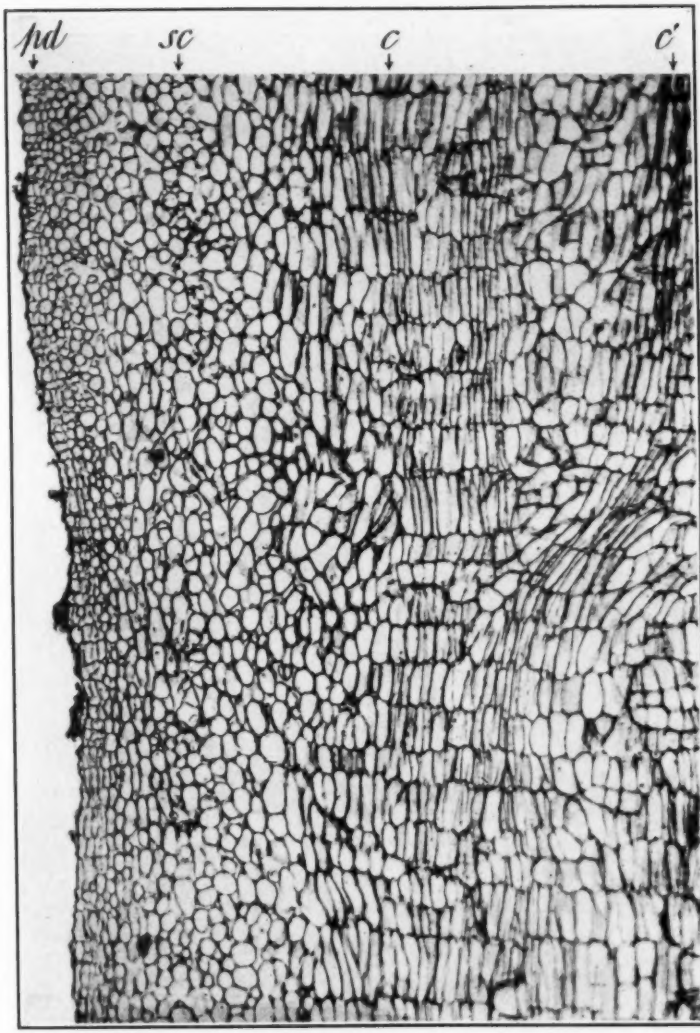


FIG. 19.—Radial section through periphery of mature beet, showing periderm, cortex, and cambium of the first ring. *pd*, periderm; *s. c*, secondary cortex; *c*, cambium; *c'*, cambium of second ring. × 270

The development and growth of the individual rings follows, in principle, the differentiation processes of ordinary collateral bundles, but these are modified because of the interpolation of large amounts of storage parenchyma inside the bundles.

The youngest ring, nearest the periphery, is composed of a multiseriate cambium in which here and there a few cells have matured into small groups of sieve tubes and companion cells (fig. 21). In the second ring phloem differentiation becomes quite general, and

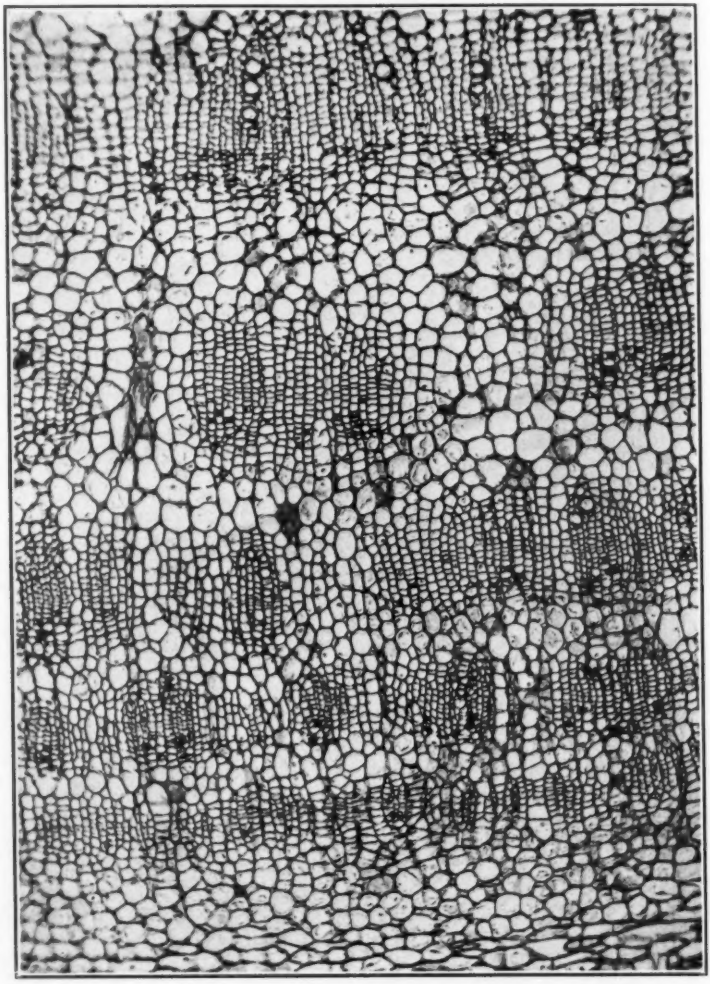

FIG. 20.—Cross section of peripheral zone of mature beet. The rings are composed mostly of undifferentiated cambium and some phloem. × 90

even in subsequent ones the extensive development of phloem dominates the anatomical picture. Following the differentiation of the first sieve tubes, phloem parenchyma is formed, and this subsequently divides and enlarges, pushing the first-formed groups of sieve tubes farther away from the vascular ring and finally obliterating them.

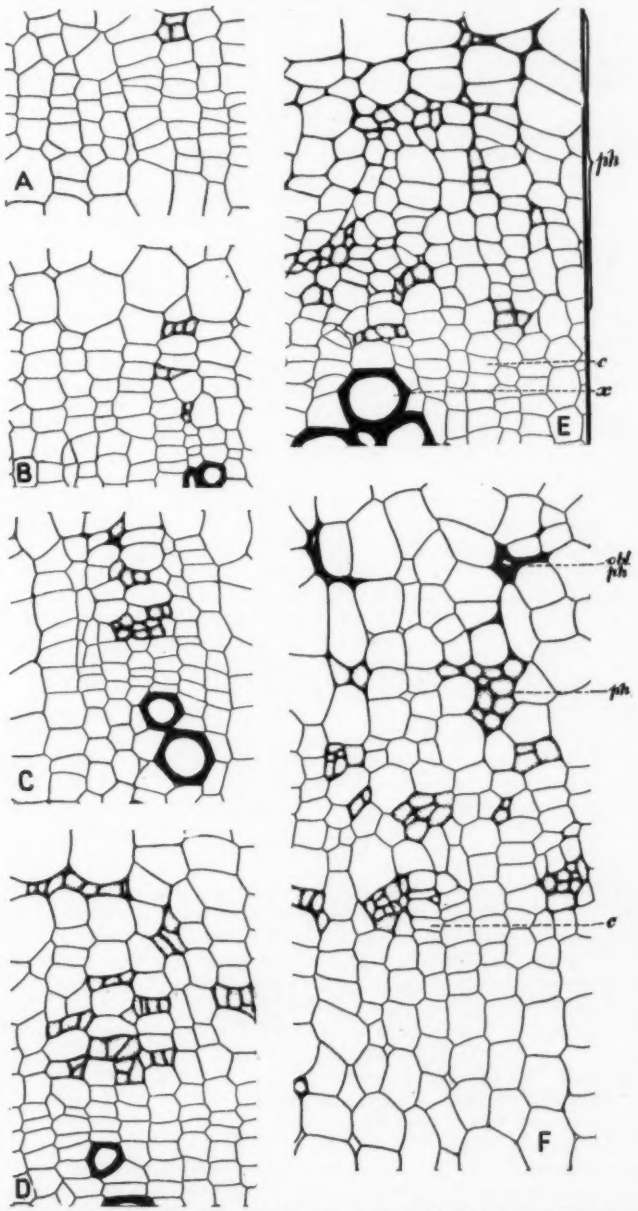


FIG. 21.—Ontogeny of the phloem of sugar beet. × 317. *A*, first peripheral ring; *B*, second ring; *C*, third ring; *D*, fourth ring; *E*, fifth ring; *F*, fifth ring, but from a different part of the beet. The phloem shows a very marked degree of development compared to the xylem. The outermost phloem groups in *F* are already obliterated. × 320

In general, the groups of sieve tubes appear in narrow radial bands broken up radially and tangentially by the larger cells of the phloem parenchyma.

Centripetally the cambium develops a broad band of parenchyma in which appear the first xylem cells; this occurs usually only after considerable phloem has been formed. In certain bundles, phloem and xylem differentiation appears to be reciprocal, but most often the appearance of xylem is belated. After the first few xylem cells have been formed, the cambium matures additional parenchyma and occasionally a xylem cell. Cell division in the parenchyma between the xylem continues irregularly, and as a result the xylem cells became displaced radially and tangentially and project far into the parenchyma (fig. 22). The cambium between the bundles gives rise to large-celled medullary-ray tissue. Where bundles are very close together the ray cells are small and radially elongated.

The rings of vascular tissue are separated by broad bands of storage parenchyma. In the peripheral zone these bands are not more than one or two cells wide, and in places the phloem of the next inner ring abuts on the cambium of the outer ring (fig. 23). Since each supernumerary cambium is the direct descendant of the next older cambium, and since the first-differentiated phloem groups are sieve tubes, the band of interzonal parenchyma is ultimately the product of centripetal cambial growth.

A close examination of the interzonal parenchyma shows that it is in reality made up of three regions: An outer, comparatively broad zone, containing scattered xylem cells; an intermediate, purely parenchymatous zone; and an inner zone containing obliterated phloem (fig. 2, A). As xylem differentiation is strictly centripetal the innermost xylem cells constitute the inner limit of the first zone, which is thus closely related to the vascular ring. The broad intermediate zone has been formed by cell division and cell enlargement of the parenchyma cells differentiated by the cambium previous to xylem formation. Finally, the inner zone is delimited centrifugally by the obliterated phloem and consists chiefly of phloem parenchyma. It is therefore the product of centrifugal growth of the older ring.

## SUMMARY

The sugar beet is an elongated more or less pear-shaped body composed morphologically of crown, neck, and root. In cross section it appears to be made up of a number of annular zones or rings of growth, separated by bands of storage parenchyma. Only the four or five inner rings mature their tissues, while the peripheral ones remain in a more or less meristematic condition.

The center of the beet is occupied by a solid, more or less star-shaped, core of which the innermost part constitutes the primary xylem plate. The latter is either directly continuous with the secondary xylem of the core, or is separated from it by a concentric ring of parenchyma of varying width.

The young seedling beet has a central strand of vascular tissue inclosed by a cortex and bounded at the periphery by an epidermis. The central strand is made up of a diarch protoxylem plate with alternating phloem groups, a single-layered pericycle and a band of interstitial parenchyma between xylem and phloem.

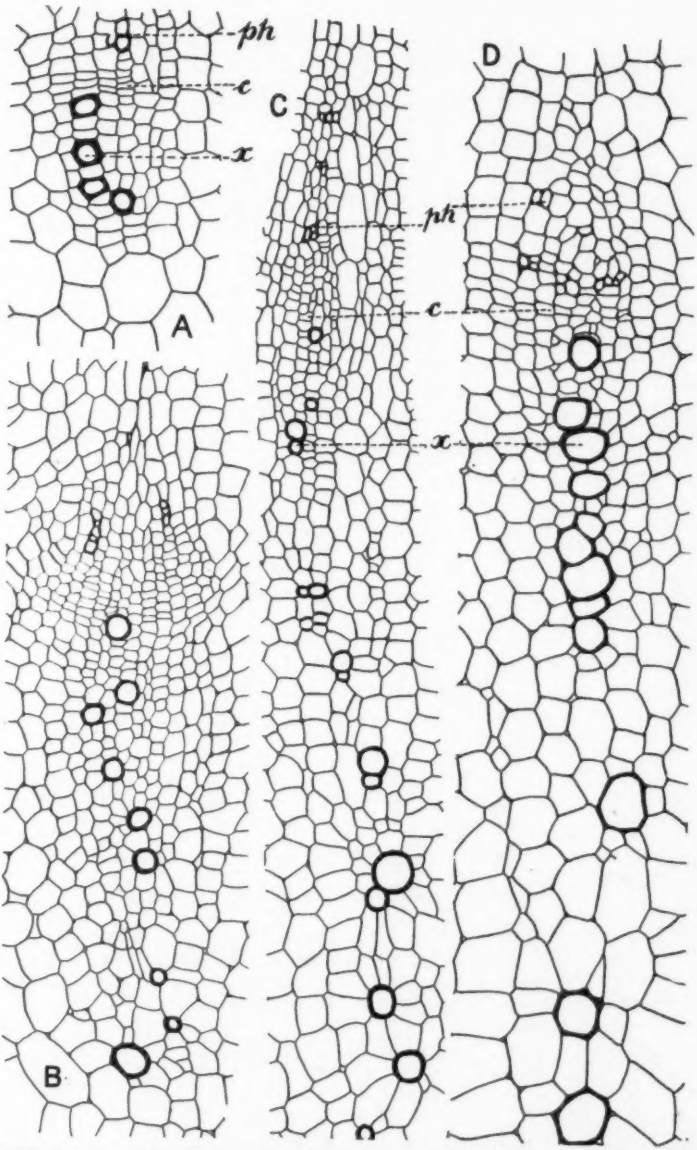


FIG. 22.—*A*. Young peripheral bundle of mature beet. × 510. *ph*, phloem; *c*, cambium; *r*, xylem. *B*. Older bundle, with parenchyma developing between the xylem cells. × 100. *C*. Very narrow bundle of the same age. A large amount of parenchyma has become interpolated between the vessels, forcing them farther and farther apart. × 100. *D*. Bundle of an older ring, which shows a larger amount of xylem. × 180

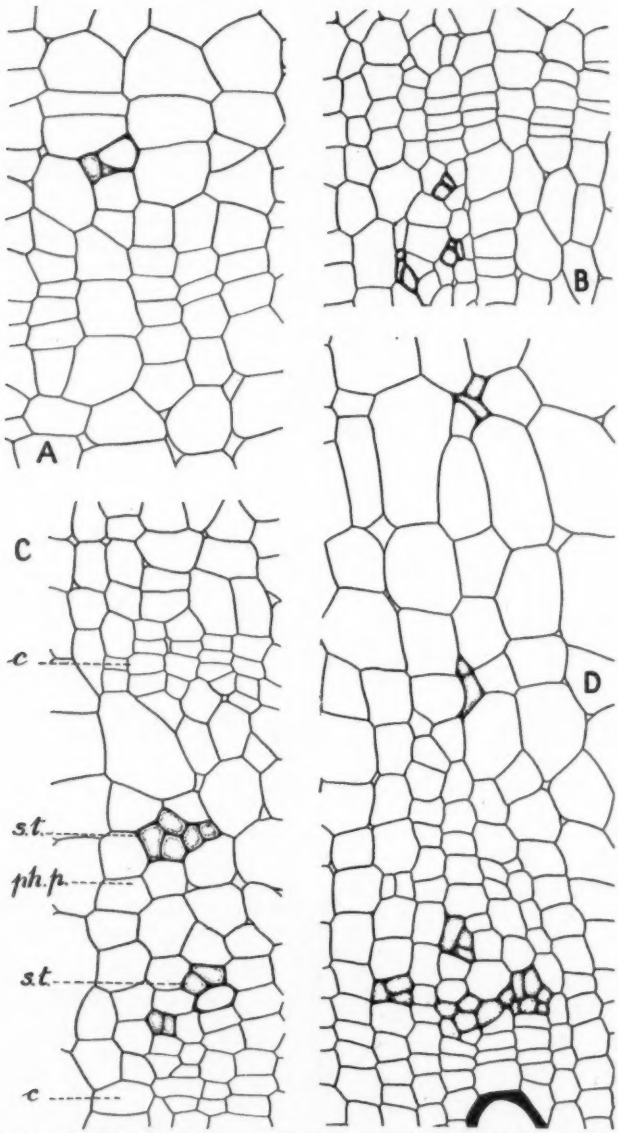


FIG. 23.—Ontogeny of the interzonal parenchyma of beet. *A*. Peripheral zone of an actively growing beet. The outermost ring comprises only one layer of cambium. The cambium of the second ring has already formed a group of sieve tubes and parenchyma. Note that the group of sieve tubes lies next to the cambium of the first ring. *B*. A more advanced stage than in *A*. *C*. The outer cambium has formed parenchyma centripetally. In the next inner ring the first sieve tubes have become separated from later-formed ones by phloem parenchyma cells. *c*, cambium; *s. t.*, sieve tube; *ph. p.*, phloem parenchyma. *D*. A more advanced stage. The first-formed sieve tubes project far into the parenchyma of the ring

Secondary growth of the beet involves the activity of a primary cambium and of secondary cambiums.

The primary cambium gives rise to the innermost annual ring in the beet. It arises in the interstitial parenchyma, except, of course, in the region opposite the two protoxylem points where it is derived from the pericycle.

The first secondary cambium arises in root and lower hypocotyl from cells of the primary phloem parenchyma. Occasionally undifferentiated procambium cells between pericycle and phloem parenchyma contribute to its development. In the upper hypocotyl it is derived from the pericycle, and in the intermediate hypocotyl both pericycle and phloem parenchyma contribute to its development. In the region opposite the protoxylem points, both primary and secondary cambiums are descendants from pericycle tissue.

All other supernumerary cambiums stand for the most part in direct lineage with the first secondary cambium.

The periderm is derived from the pericycle. It forms phellogen and phelloderm cells in reciprocal fashion.

Practically all the supernumerary cambiums for the annular rings of the mature beet have been formed while the latter is no thicker than a lead pencil. The enormous increase in the diameter of the beet is due to cell division and cell enlargement taking place simultaneously in all the rings.

The degree of development attained by the vascular tissue of a ring and the separating band of interzonal parenchyma varies greatly with different beets. In any given one, however, the innermost rings have the broadest band of parenchyma.

The interzonal parenchyma in its entirety is made up of three regions: An outer zone containing scattered xylem cells, a central purely parenchyma zone, and an inner zone containing obliterated phloem. The first two zones have been formed by centripetal growth of the outer ring, while the third zone is the product of centrifugal growth of the older inner ring.

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# INSECTICIDAL VALUE OF CERTAIN WAR CHEMICALS AS TESTED ON THE TENT CATERPILLAR [1]

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## INTRODUCTION

At the request of the Chemical Warfare Service of the War Department, the writer was detailed by the Bureau of Entomology of the Department of Agriculture to make a study of the chemical compounds developed by the Chemical Warfare Service during and since the World War, to determine their value as insecticides. The War Department has developed many new and interesting compounds, but the majority of them seem to have no practical value as insecticides and hence have not been studied in detail. All of the available compounds that were thought to have any possible value as stomach poisons, contact insecticides, or fumigants were tested for toxicity to insects and host plants. This paper is a general report of the experiments conducted with the various materials to learn something of their usefulness as stomach poisons and contact insecticides. The report on fumigation will be presented later.

Owing to the fact that a rather large number of compounds were to be tested, it was decided to conduct the experiments in such a way that only a general idea of the toxicity of the compounds to insects and plants might be obtained, no attempt being made to determine the exact toxicity of any compound. It was considered that the results obtained with 10 to 25 insects in each test would be sufficient to furnish a basis for further study.

The work reported here was conducted in cooperation with the Chemical Warfare Service at Edgewood Arsenal, Md., in 1924.

## EXPERIMENTS ON STOMACH POISONING

Eastern tent caterpillars (*Malacosoma americana* Fab.) were very abundant at the Arsenal, and as they are considered to be somewhat resistant to arsenicals, they were used in this study, and proved to be excellent material.

The chemical compound to be tested as a stomach poison was sprayed or dusted on the leaves of small twigs of wild cherry, the favorite food plant of this insect. The sprayed branches were placed in vials of water. The vials were then inclosed in cylindrical wire cages 4 inches in diameter and 10 inches in height. Twenty-five third-grown to half-grown caterpillars were put into each cage with the sprayed foliage. Notes were taken daily, the relative amount of foliage consumed and the time of death being carefully noted in each case.

[1] Received for publication Feb. 2, 1926; issued July, 1926.

[2] The writer expresses his appreciation to A. L. Quaintance and C. H. Richardson of the Bureau of Entomology of the United States Department of Agriculture, under whose general direction this work was conducted; and to W. A. Taylor, formerly of the Chemical Warfare Service of the United States War Department, for the formulas of the chemical compounds used, and to H. C. Knight and many other chemists of the Chemical Warfare Service for helpful suggestions.

CHEMICAL COMPOUNDS USED

The compounds tested were largely organic arsenicals, many of which were the oxides of gases and smokes developed during the World War. The cost of some of these compounds would prohibit their use as insecticides, but in this study the cost was not taken into consideration.

Following is a list of the compounds used, with a brief description of some of their chemical and physical properties:

1. DIPHENYLAMINO ARSENIOUS OXIDE, $[NH(C_6H_4)_2AS]_2O$. A light-yellow amorphous compound, finely divided into extremely small particles. It mixes well with water, if a paste is first made with a small amount of water and more water is then added slowly to this paste until the desired dilution is reached. This chemical spreads evenly over the foliage, and remains well in suspension. Great caution must be used in handling it, for inhalation of it irritates the nasal passages and throat and causes sneezing.

2. DIPHENYL ARSENIOUS OXIDE, $(C_6H_5)_2As.\ O.\ As\ (C_6H_5)_2$. A white powder of very fine crystals which settle out very rapidly from an aqueous suspension and collect in small patches on the sprayed foliage.

3. CHLOROVINYL ARSENIOUS OXIDE, $ClHC=CHAsO$. A white flaky crystalline compound. Does not mix well with water; it settles very rapidly in water, and the spray deposit on foliage is uneven and patchy. If the crystals remain on the skin they cause a slight irritation, and in some cases blistering. The fumes are very irritating to the nose and throat.

4. CALCIUM ETHYL ARSONATE (calcium salt of ethyl arsonic acid), $CaC_2H_5AsO_3$. A very fine powder which mixes readily with water and remains well in suspension. The spray deposit is spread evenly over the leaf.

5. ETHYLENE DITHIO-CYANATE, $NCSCH_2CH_2SCN$. A heavy crystalline material, which settles very quickly after being mixed with water. It does not form an even deposit over the leaf.

6. 2–4–6 TRICHLOROPHENYL BENZYLCHLORAMINE, $Cl_3C_6H_2NClCH_2C_6H_5$. A light-brown gummy compound, which forms small pellets when mixed with water.

7. 2–4–6 TRICHLOROPHENYL ACETYL CHLORAMINE, $Cl_3C_6H_2NClCOCH_3$. Is similar to trichlorophenyl benzylchloramine.

8. CALCIUM METHYL ARSONATE (calcium salt of methyl arsonic acid), $CaCH_3AsO_3$. Similar to calcium ethyl arsonate.

9. PHENYL ARSENIOUS OXIDE, $C_6H_5AsO$. Similar to diphenyl arsenious oxide.

10. DIMETHYL ANILINO ARSENIOUS OXIDE, $(CH_3)_2NC_6H_4AsO$.

11. p–DIMETHYL AMINO BENZALDEHYDE, $(CH_3)_2NC_6H_4CHO$.

12. COPPER STEARATE, COPPER RESINATE, MERCURY STEARATE, LEAD STEARATE, LEAD RESINATE, MERCURY RESINATE, and ZINC RESINATE, were very fine powders which had been passed through a 160-mesh sieve. They were exceedingly hard to mix with water. Mixture with water was accomplished only by first making a paste and then adding slowly the required amount of water. These materials spread very well over the entire leaf surface, forming a thin even film.

EFFECT ON TENT CATERPILLAR AND THE BEAN PLANT

The effect of the compound on the plant could not be determined where wild cherry was used, because the branches were detached from the plant. Beans were used because they could easily be grown in pots, could be handled without difficulty, and are very susceptible to injury by arsenical compounds.

Table 1 gives a list of the compounds used and their comparative toxicity to tent caterpillars and host plants. In Table 1 "concentration" is the amount in grams of the material in 100 c. c. of distilled water, except where dusts were used. Where dusts were used the material was mixed with kaolin and applied in the proportion given, as, for example, one part of material to five of kaolin. The time in days refers to the time between the first feeding and the death of the last insect, or to the time when the experiment was closed.

Control experiments were conducted with unsprayed foliage so that the normal death rate might be observed. Lead arsenate was used as the standard for comparison with the materials mentioned above.

TABLE 1.—*Comparative toxicity of a number of organic compounds to tent caterpillars and bean plants when the compounds were applied as sprays to kill by stomach poisoning*

| Material used | Concentration (gms. per 100 c. c. of water) | Number of insects in test | Number dead | Days from first feeding to last death | Effect on plant | Foliage eaten |
|---|---|---|---|---|---|---|
| Diphenylamino arsenious oxide. | 0.5 | 25 | 25 | 5 | None | Small amount. |
| Do | 1.0 | 25 | 25 | 4 | do | Do. |
| Do | 2.0 | 25 | 25 | 7 | do | Do. |
| Do | (a) | 25 | 25 | 6 | Very slight | Do. |
| Do | (b) | 25 | 25 | 6 | None | Do. |
| Diphenyl arsenious oxide. | .5 | 25 | 25 | 4 | Severely burned | Do. |
| Do | 1.0 | 25 | 25 | 4 | do | Do. |
| Do | 2.0 | 25 | 25 | 4 | do | Do. |
| Do | .1 | 25 | 25 | 6 | do | Do. |
| Do | .25 | 25 | 25 | 3 | do | Do. |
| Do | (a) | 25 | 25 | 3 | do | Do. |
| Do | (b) | 25 | 25 | 5 | do | Do. |
| Chlorovinyl arsenious oxide. | .1 | 25 | 25 | 7 | do | |
| Do | .25 | 25 | 23 | 5 | Completely burned | |
| Do | .5 | 25 | 15 | 4 | do | Experiment closed |
| Do | 1.0 | 25 | 20 | 4 | do | |
| Do | 2.0 | 25 | 17 | 4 | do | |
| Control | | 25 | 3 | 9 | Food replaced several times. | |
| Copper stearate | .1 | 25 | 20 | 19 | None | All. |
| Do | .25 | 25 | 12 | 16 | do | Do. |
| Do | .5 | 25 | 9 | 16 | do | Do. |
| Do | 1.0 | 25 | 19 | 24 | do | Do. |
| Copper resinate | .1 | 25 | 9 | 9 | do | Do. |
| Do | .25 | 25 | 9 | 9 | do | Do. |
| Do | .5 | 25 | 8 | 10 | do | Do. |
| Do | 1.0 | 25 | 22 | 38 | do | Do. |
| Mercury stearate | .1 | 25 | 11 | 15 | do | Do. |
| Do | .25 | 25 | 14 | 9 | do | Do. |
| Do | .5 | 25 | 24 | 13 | do | Very little. |
| Do | 1.0 | 25 | 15 | 9 | do | Experiment closed (leaves fell from plant, but not because of burning). |
| Lead arsenate | .1 | 25 | 25 | 13 | do | One-half. |
| Do | .25 | 25 | 25 | 11 | do | One-third. |
| Do | .5 | 25 | 25 | 11 | do | Do. |
| Do | 1.0 | 25 | 25 | 16 | do | Do. |
| Control | | 25 | 21 | 14 | do | Foliage replaced. |

[a] Dust (pure). [b] Dust with kaolin (1–10). [c] Dust with kaolin (1–5).

TABLE 1.—*Comparative toxicity of a number of organic compounds to tent caterpillars and bean plants when the compounds were applied as sprays to kill by stomach poisoning*—Continued

| Material used | Concentration (gms. per 100 c. c. of water) | Number of insects in test | Number dead | Days from first feeding to last death | Effect on plant | Foliage eaten |
|---|---|---|---|---|---|---|
| Lead stearate | 0.1 | 25 | 2 | 3 | None | All. |
| Do | .25 | 25 | 1 | 3 | do | Do. |
| Do | .5 | 25 | 0 | 3 | do | Do. |
| Do | 1.0 | 25 | 2 | 9 | do | Do. |
| Lead resinate | .1 | 25 | 11 | 8 | do | Do. |
| Do | .25 | 25 | 10 | 11 | do | Do. |
| Do | .5 | 25 | 11 | 9 | do | Do. |
| Do | 1.0 | 25 | 12 | 8 | do | Do. |
| Chlorovinyl arsenious oxide. | [b] | 25 | 14 | 4 | Severely burned | Experiment closed. |
| Do | [d] | 25 | 19 | 4 | do | Do. |
| Lead arsenate | .5 | 25 | 25 | 5 | None | Fair amount. |
| Do | 2.0 | 25 | 25 | 3 | do | Do. |
| Kaolin | [a] | 25 | 1 | 3 | do | All. |
| Control | | 25 | 0 | 9 | do | Foliage replaced. |
| Phenylarsenious oxide | .1 | 25 | 25 | 5 | Severely burned | |
| Do | .25 | 25 | 15 | 7 | do | |
| Do | .5 | 25 | 25 | 4 | do | |
| Do | 1.0 | 25 | 25 | 4 | do | |
| Calcium methyl arsonate. | .1 | 25 | 0 | 3 | None | All. |
| Do | .25 | 25 | 25 | 5 | Severely burned | Little. |
| Do | .5 | 25 | 15 | 3 | do | Experiment closed. |
| Do | 1.0 | 25 | 25 | 7 | do | |
| Lead arsenate | .1 | 25 | 25 | 5 | None | Fair amount. |
| Do | .25 | 25 | 25 | 4 | do | |
| Do | .5 | 25 | 25 | 6 | do | |
| Do | 1.0 | 25 | 25 | 8 | do | |
| Calcium ethyl arsonate. | .1 | 25 | 20 | 13 | Severely burned | Considerable. |
| Do | .25 | 25 | 18 | 6 | do | |
| Do | .5 | 25 | 25 | 8 | do | |
| Do | 1.0 | 25 | 25 | 8 | do | |
| Ethylene dithio-cyanate. | .1 | 25 | 9 | 7 | None | Considerable. |
| Do | .25 | 25 | 0 | 2 | do | All. |
| Do | .5 | 25 | 0 | 1 | do | Do. |
| Do | 1.0 | 25 | 0 | 2 | do | Do. |
| 2-4-6 Trichlorophenyl benzylchloramine. | 1.0 | 25 | 24 | 15 | do | Do. |
| Do | 2.0 | 25 | 10 | 10 | do | Do. |
| 2-4-6 Trichlorophenyl acetyl chloramine. | 1.0 | 25 | 5 | 3 | Tender leaves slightly burned. | Do. |
| Do | 2.0 | 25 | 0 | 5 | Slightly burned | Do. |
| p-Dimethyl amino benzaldehyde. | .1 | 25 | 3 | 8 | None | Do. |
| Do | .25 | 25 | 7 | 8 | do | Do. |
| Do | .5 | 25 | 3 | 8 | do | Do. |
| Do | 1.0 | 25 | 2 | 8 | do | Do. |
| Dimethyl anilino arsenious oxide. | .1 | 25 | 15 | 7 | Slightly burned | Do. |
| Do | .25 | 25 | 25 | 8 | do | One-third. |
| Do | .5 | 25 | 25 | 11 | Severely burned | One-half. |
| Do | 1.0 | 25 | 25 | 12 | do | Do. |
| Mercury resinate | .1 | 25 | 0 | 6 | do | Do. |
| Do | .25 | 25 | 3 | 8 | do | Do. |
| Do | .5 | 25 | 2 | 8 | do | Do. |
| Do | 1.0 | 25 | 9 | 8 | do | Do. |
| Zinc resinate | .1 | 25 | 0 | 5 | do | Do. |
| Do | .25 | 25 | 0 | 5 | do | Do. |
| Do | .5 | 25 | 1 | 12 | do | Do. |
| Do | 1.0 | 25 | 0 | 3 | do | Do. |

[a] Dust (pure). [b] Dust with kaolin (1–10). [d] Dust with kaolin (1–25).

Diphenylamino arsenious oxide proved to be the most promising of the materials tried, it being about equal to lead arsenate in toxicity to the insect, and was not injurious to the bean plants even in strong concentrations. When the pure material was dusted on the plant slight injury developed after several days, especially to the tender

leaves and growing tips. Mixed with kaolin in the proportion of 1 part to 10 parts of kaolin, there was no injury to the plants, and a 100 per cent kill resulted in six days.

Diphenyl arsenious oxide chlorovinyl arsenious oxide, and phenyl arsenious oxide, proved to be very toxic to the insect but were also toxic to the plant. Saturated solutions of these materials were made by allowing the compound to remain in water overnight and then filtering it. When this filtrate was used as a spray it burned the plant severely.

Diphenyl arsenious oxide was used with equal parts of hydrated lime. The lime prevented plant injury, but it also greatly reduced the toxicity of the compound to the insect.

When phenyl arsenious oxide was used with lime the injurious effect upon the plant was greatly lessened; severe injury resulted, however, in some cases. The addition of lime reduced the toxicity of the compound to the insect.

Copper stearate and copper resinate, although comparatively nontoxic, seemed to have a decidedly repellent effect upon the insect. It required from 9 to 38 days for the caterpillars to consume the foliage given them, whereas the control insects consumed the same amount of foliage in from 1 to 3 days. It is the opinion of the writer that many of the insects in these tests did not die from poisoning but died from starvation because they would not eat the sprayed foliage. Both copper stearate and copper resinate have excellent spreading and adhering qualities, and it may be practicable to use them as sprays for tender foliage that can not be treated with an arsenical.

## EXPERIMENTS ON CONTACT POISONING

Experiments were conducted to determine the toxicity of certain chemical compounds as contact insecticides. The same compounds were used in these tests as were used in the experiments in stomach poisoning. The compounds to be tested were sprayed on half-grown tent caterpillars. The caterpillars were allowed to dry, and they were then placed on unsprayed cherry foliage. Ten larvae were used in each test. Notes were taken daily, and the rate of death observed. Table 2 gives a summary of the results of these experiments.

Diphenylamino arsenious oxide, diphenyl arsenious oxide, and chlorovinyl arsenious oxide proved to be toxic as contact insecticides as well as stomach poisons. However, diphenyl arsenious oxide and chlorovinyl arsenious oxide were extremely toxic to bean plants (Table 1).

Diphenylamino arsenious oxide seems to be a promising contact insecticide as well as stomach poison. Further experiments with this compound are now in progress.

TABLE 2.—*Comparative toxicity to tent caterpillars of a number of compounds tested as contact insecticides*

| Material used | Concentration (grams per 100 c. c. of water) | Number of insects in test | Number dead | Days from treatment to last death |
|---|---|---|---|---|
| Diphenylamino arsenious oxide | 0.5 | 10 | 10 | 2 |
| Do | 1.0 | 10 | 10 | 4 |
| Do | 2.0 | | | |
| Diphenyl arsenious oxide | .1 | 10 | 10 | 3 |
| Do | .25 | 10 | 10 | 3 |
| Do | .5 | 10 | 10 | 2 |
| Do | 1.0 | 10 | 10 | 2 |
| Do | 2.0 | 10 | 10 | 2 |
| Chlorovinyl arsenious oxide | .1 | 10 | 9 | 3 |
| Do | .25 | 10 | 10 | 1 |
| Do | .5 | 10 | 10 | 1 |
| Do | 1.0 | 10 | 10 | 1 |
| Do | 2.0 | 10 | 10 | 1 |
| Phenyl arsenious oxide | .1 | 10 | 0 | 5 |
| Do | .25 | 10 | 0 | 5 |
| Control | | 10 | 0 | 5 |
| Calcium methyl arsonate | .1 | 10 | 0 | 3 |
| Do | .25 | 10 | 1 | 3 |
| Do | 1.0 | 10 | 0 | 3 |
| Calcium ethyl arsonate | .1 | 10 | 1 | 5 |
| Do | .25 | 10 | 1 | 5 |
| Do | 1.0 | 10 | 0 | 3 |
| Do | .1 | 10 | 1 | 5 |
| Do | .25 | 10 | 1 | 5 |
| Do | .5 | 10 | 10 | 5 |
| Do | 1.0 | 10 | 6 | 5 |
| Ethylene dithio-cyanate | .1 | 10 | 1 | 5 |
| Do | .25 | 10 | 1 | 5 |
| Do | .5 | 10 | 1 | 5 |
| 2-4-6 Trichlorophenyl benzylchloramine | 1.0 | 10 | 0 | 3 |
| Do | 2.0 | 10 | 0 | 3 |
| 2-4-6 Trichlorophenyl acetyl chloramine | .1 | 10 | 1 | 3 |
| Do | .25 | 10 | 0 | 3 |
| Do | .5 | 10 | 0 | 3 |
| Do | 1.0 | 10 | 0 | 10 |
| p-Dimethyl amino benzaldehyde | .1 | 10 | 0 | 10 |
| Do | .25 | 10 | 0 | 10 |
| Do | 1.0 | 10 | 0 | 10 |
| Dimethyl anilino arsenious oxide | .1 | 10 | 2 | 8 |
| Do | .25 | 10 | 5 | 8 |
| Do | .5 | 10 | 5 | 8 |
| Do | 1.0 | 10 | 9 | 6 |
| Copper stearate | .1 | 10 | 2 | 5 |
| Do | .25 | 10 | 2 | 5 |
| Do | .5 | 10 | 2 | 5 |
| Do | 1.0 | 10 | 0 | 5 |
| Copper resinate | .1 | 10 | 1 | 8 |
| Do | .25 | 10 | 3 | 8 |
| Do | .5 | 10 | 0 | 8 |
| Mercury stearate | .1 | 10 | 0 | 8 |
| Do | .25 | 10 | 0 | 7 |
| Do | .5 | 10 | 2 | 7 |
| Do | 1.0 | 10 | 5 | 3 |
| Control | | 10 | 0 | 7 |
| Lead stearate | .1 | 10 | 1 | 8 |
| Do | .25 | 10 | 1 | 8 |
| Do | .5 | 10 | 0 | 8 |
| Do | 1.0 | 10 | 1 | 8 |

## SUMMARY

In a series of experiments, a number of organic compounds developed by the Chemical Warface Service were tested both as stomach poisons and contact insecticides, on third-grown to half-grown eastern tent caterpillars (*Malacosoma americana* Fab.).

The effect of the insecticide upon the host plant was determined by treating bean plants with the material to be tested. Most of the compounds that were toxic to insects proved to be so toxic to the plants as to have no practical value.

As a stomach poison, diphenylamino arsenious oxide was equal in toxicity to lead arsenate, and it was not injurious to the bean plants. It also has some promise as a contact insecticide.

# RELATION OF THE MANNER OF FAILURE TO THE STRUCTURE OF WOOD UNDER COMPRESSION PARALLEL TO THE GRAIN[1]

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## PURPOSE OF STUDY

It is frequently noted in pieces of wood which have failed in compression parallel to the grain, that the line of failure is more or less inclined on the tangential or flat-grain faces but is practically at right angles to the grain on the radial or edge-grain faces. (See figs. 5 and 6.) This seems to be true for a great many species of both hardwoods and softwoods. Evidently there is something about the structure of the wood which tends to cause the failure to be inclined in the one direction. That the plane of failure would be inclined in one direction or another might be expected, since experiments show that materials which, like wood, are neither fully plastic nor easily pulverizable fail along inclined planes when subjected to compression, the angle of rupture being such as to cause failure under the least load necessary to effect a change. The purpose of this study was to determine what there is about the arrangement of the various tissues of wood, or the structure of the individual cells, which almost constantly produces an inclination of the plane of failure in the tangential direction.

## MATERIAL

The material for study was chosen from both softwoods and hardwoods available at the Forest Products Laboratory, Madison, Wis. It consisted of 88 pieces of southern yellow pine, 136 of Douglas fir, 100 of Sitka spruce, 110 of oak, 25 of ash, 16 of red gum, 15 of mahogany, 14 of sugar maple, 10 of birch, and 10 of balsa (an exceedingly soft and light tropical wood).

The test pieces had, in most cases, the standard size of 2 by 2 by 8 inches. Some, however, were cut with different cross-sectional dimensions, to see if that made any difference in the manner of failure—with negative results. All specimens were subjected to compression in testing machines according to the standard procedure at the Forest Products Laboratory.

The specimens were in an air-dry condition, except for some of the Douglas fir specimens, which were well above the fiber-saturation point. The density and the maximum crushing strength developed are on record for nearly all.

[1] Received for publication Nov. 21, 1925; issued July, 1926. These investigations were carried on under the direction of Arthur Koehler, in charge, Office of Wood Technology, Forest Products Laboratory, Forest Service, United States Department of Agriculture, Madison, Wis.

Specimens which did not present strictly radial and tangential surfaces, as tested, were afterwards split along the radius and tangent of the annual rings. A surface slightly divergent from the radius might show an inclined failure on the presumably radial surface, whereas when the block was split exactly radially the failure appeared practically at right angles to the fibers on the split surface, thus conforming with the basic premise of the investigation.

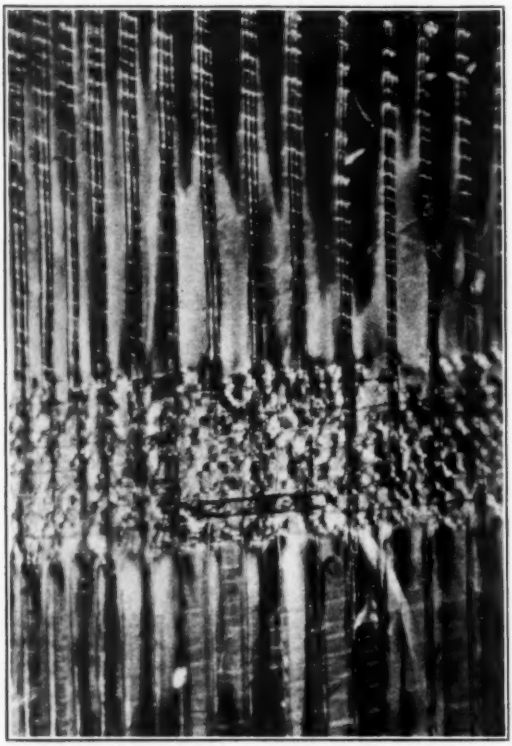

FIG. 1.—Slip planes in fiber walls of Sitka spruce. (The transverse band near the middle is a medullary ray.) Photographed by polarized light. ×156

Longitudinal microscopic sections, including failures in various stages of development, were prepared from many of the test pieces, and different stains were used to bring out contrast. Soon, however, the examination was performed almost entirely with the help of polarized light, which was particularly useful as a rapid and vivid means of discovering the existence of initial failures and of even more minute changes in the cell wall.

## SIGNIFICANCE OF SLIP-PLANES IN THE FIBERS

Studying the character of the gross failures in radial and tangential sections with the question in mind, "How and from what do they originate?" one naturally goes to the earliest stages of failure. Immediately one's attention is drawn to the fact that the cell walls show changes attributable to stress, even before a real failure can be considered to be present; and from that observation the necessity of studying the initial changes is obvious.

Robinson [2] observed what appear to be the preliminary stages of failure in compression along the grain, to which he gave the name of

[2] ROBINSON, W. THE MICROSCOPICAL FEATURES OF MECHANICAL STRAINS IN TIMBER AND THE BEARING OF THESE ON THE STRUCTURE OF THE CELL-WALL IN PLANTS. Roy. Soc. [London] Phil. Trans. (B) 210: 57. 1920.

"slip lines" or "slip planes." As seen in conifers, he defined them as "the changes that lead to deformation and consist in appearance of extremely fine but sharply defined cracklike lines in the walls of the tracheids."

Slip planes corresponding to those described and illustrated by Robinson can be seen with extraordinary clearness in the fiber walls shown in Figure 1, which represents a radial section of Sitka spruce photographed by polarized light. In the cell walls cut through lengthwise (upper part of figure) each slip plane appears as a short bright line extending across the wall at an angle of about 70° with the longitudinal axis of the fiber. The slope may be in either direction, though only one is clearly shown here, and occasionally the slip planes may cross each other, forming X-shaped hatchings. In the lower part of Figure 1 a surface view of the cell walls shows the slip planes extending around the fiber at a slight incline.

The extraordinary brightness of the slip planes in Figure 1 may be due either to the relative thinness of the section from which the photograph was made or to the fact that the stick from which the section was cut had been subjected to tension after compression, for wood so tested often reveals the slip planes with unusual brightness. A probable explanation of the latter effect is offered in the third footnote.[3]

There seems to be a wide variation in the brightness as well as the number of slip planes in woods of different species. In general it can be said that the thicker the cell walls and the thinner the sections the more readily they can be observed.

Slip planes are considered the first indication that the wood has been subjected to severe longitudinal compression, either artificially or naturally, for the following reasons:

1. They are much more numerous in parts of cell walls which have actually failed in compression than in other parts. (See fig. 2.)

2. They often are associated with a little displacement or offset of the fiber wall. There is a noticeable similarity between this kind of displacement and the gross displacement of the whole test piece when it has finally given way under compression. The presence of slip planes is strong presumptive evidence that the individual fiber has been injured—that something has given way locally.[3]

3. The slip planes take up stains selectively just as do the larger injuries to the cell walls.

4. Slip planes are common in many woods, whether intentionally subjected to stresses or not, as has been found from the study of microscopic sections taken from both hardwoods and softwoods. When present in wood not previously subjected to any testing, they are probably to be considered as due to stresses resulting from the weight of the tree, wind action, felling or rough handling, or uneven longitudinal shrinkage. That the last-named is not necessarily the cause, however, was shown by the presence of slip planes in sections

[3] It may be for this reason that slip planes have been found to be exceptionally bright (under polarized light) in sections cut from pieces subjected to tension. Under tension, naturally, the injured parts are stretched, thus forming a broader zone which makes them more conspicuous.

Contrary to Robinson's opinion, however, it is doubtful that slip planes are produced in tension parallel to the grain. Their presence in specimens subjected to tensile stresses does not prove that they were formed while those stresses were operative. The fact that slip planes were found to be no more numerous in the region of failure in specimens tested in tension than in wood not artificially stressed indicates that they do not develop in tension.

cut from green wood and mounted for observation in water.[4] That severe compression stresses may occur in wood before use or test is shown by the advanced compression failures which have been found in new lumber. This phenomenon is by no means very exceptional and has been recognized again and again.[5]

5. To make certain that the slip planes were not formed by the shearing action of the knife in cutting the longitudinal sections of the wood parallel with the fibers, sections were cut with the knife passing through the wood at right angles to the fibers. This did not seem to alter in any way the number of slip planes present. Furthermore, thin and thick sections were cut, and a sharp knife and a dull knife were used, but no difference in the abundance of slip planes was observed. Even more conclusive evidence that slip

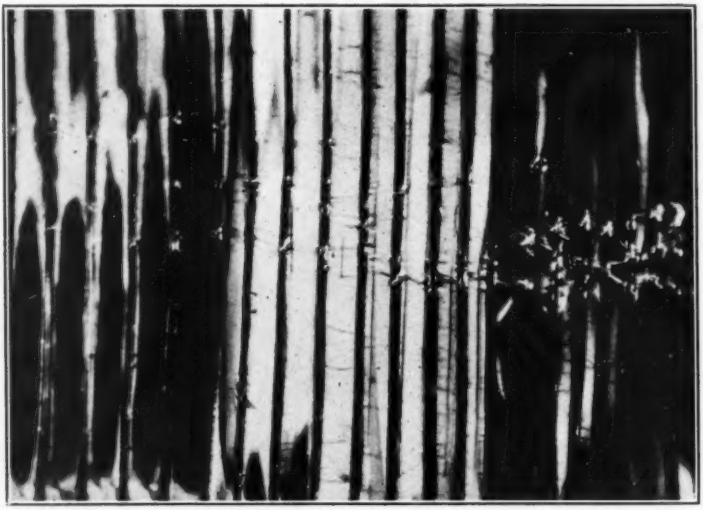

FIG. 2.—Initial compression failure made up of numerous slip planes in Sitka spruce. Photographed by polarized light. ×148

planes are not necessarily due to the shearing action of the knife in making microscopic sections is derived from their presence in carefully macerated fibers from both hardwoods and softwoods. In macerated fibers the number of slip planes may vary considerably. As a rule they are not very numerous or very bright, but they have always been found.

## FORMATION OF INITIAL COMPRESSION FAILURES

The next stage after the development of slip planes in compression parallel to the grain of wood is the formation of a localized injury,

[4] Green material was also studied to determine whether the refractive qualities of wood are changed in consequence of the treatment ordinarily given to the pieces before sectioning. The treatment consisted in boiling the blocks in water to exclude the air, then placing them in hydrofluoric acid to soften them, after which the acid was boiled out again in water and the blocks were preserved in a mixture of water, glycerin, and alcohol. Microscopic sections cut from these blocks and mounted in water showed no difference in refractive qualities under polarized light as compared with material treated in the ordinary way, nor was an appreciable difference in either the number or the character of the slip planes noted.

[5] KOEHLER, A. SELECTING WOOD FOR AIRPLANES. Sci. Amer. Sup. 88: 148–149, illus. 1919.
MARKWARDT, L. J. COMPRESSION FAILURES AS DEFECTS. Hardwood Rec. 39: 24–25, illus. 1914.

extending in a more or less definite line or zone across a number of adjacent cells. It can readily be recognized as the first definite indication of failure, and for that reason it is termed the initial failure.[6] It can not be seen without a microscope, however, and is best seen with a polarizing microscope.

This stage, and the gradual changes leading up to it, are illustrated in Figure 2. Slip planes are scattered throughout the wood, as the illustration shows, although they do not show so clearly as in Figure 1. At the extreme left of the illustration they can be seen connecting up into definite lines, which become more numerous and pronounced toward the right, especially in the summer wood. The slip planes probably had already become numerous before the initial compression failure had formed. Then they became linked up by the formation of others, producing a distinct zone of failure.

From a number of observations it can be said that the initial failure in both radial and tangential sections may extend either horizontally or in an inclined direction across the fibers—more often the latter, especially in the summer wood. At this stage no actual bending or buckling of the fibers has taken place. There is not yet anything more than the slight offset in connection with the slip planes in the individual fibers, as already described, but they are numerous and close together.

Compression failures, even when not readily apparent to the eye, should always be regarded as a source of weakness, and material in which they are present should not be used where strength is of prime importance. Under slowly applied loads they do not greatly affect the strength in compression parallel to grain, although they have a marked influence on bending properties, particularly when present on the tension side of a member. The shock-resisting ability of wood containing compression failures is even more seriously affected, complete failure of the member usually occurring along the injured section with little deformation and very suddenly. For these reasons alone it is easily seen that microscopy by polarized light is an invaluable as well as an easy method of detecting very early stages of injury or failure.

## DEVELOPMENT AND NATURE OF GROSS FAILURES

To study the development of gross failures in wood subjected to end compression, radial and tangential sections were prepared. Originally the sections were stained, since the area of failure for some reason takes certain stains[7] selectively and thus stands out from the rest of the field. But staining, however helpful it may be, is not so good as using polarized light, which, as in the case of initial failures, is sometimes almost indispensable. Under polarized light the failures stand out bright against a darker background, or vice versa. The contrast brings out every detail necessary for study in stained as well as in unstained sections. The difference in the brightness of the injured and uninjured parts is due partly to local displacements of the cell-wall material, and partly to the fact that

[6] Slip planes are of too common occurrence and usually too scattered in wood to be considered definite regions of failure.

[7] Potassium ferrocyanide, to which ferric chloride was added, was used, this giving the so-called Berlin-blue reaction. Another satisfactory stain is picro-aniline blue.

in the area forming the failure the slip-planes are so numerous and close together that the whole cell wall seems to be changed in optical properties.

Observations on microscopic sections indicate that when a certain part of the wood under stress contains a number of initial failures which have developed to a considerable extent, that part is weakened and thus forms an appropriate place for a gross failure to begin. The gross failure seems to start along, and to include, some of the initial failures, but its development is not always guided by the initial failures, for these are not continuous as a rule, whereas the gross failure is more or less so.

### GROSS FAILURES DUE TO BUCKLING OF CELL WALLS

The grosser failures which are distinct to the naked eye can be seen under the microscope to be due to buckling of the cell walls. The final extent of the buckling is dependent on how far the compression is carried, i. e., how long the increasing load is allowed to act on the test piece after the elastic limit has been passed.

It is necessary to distinguish here between buckling and crinkling, because the occurrence of these two types of failure varies according to the wood tested and also between the spring-wood and summer-wood parts of a given piece.

By buckling is understood the bending of the fibers under stress, resulting in such a deformation of the cell wall that the parts originally in one axial line are no longer in that position, but, while remaining parallel to one another, have become displaced by a certain (perhaps small) distance, the actual "buckle" forming the connection between the two parts. The deformation, or buckle, is hereafter referred to as an "offset." It is to be distinguished from the offset previously described in connection with slip planes.

Crinkling results in a permanent deformation (telescoping) in the part that crinkles, but the parts of the fibers above and below remain in the same line or almost so.

The terms "buckling" and "crinkling" are used in the same sense by Robinson.[8] They are respectively equivalent to the terms "bending" and "buckling" used by Brush.[9]

In conifers an obvious difference between the spring-wood cells and the summer-wood cells is that the latter, being smaller and thicker walled, are more likely to buckle, while the former, being thinner walled, show more or less indefinite patterns of crinkling in the early stages of the gross failure. Later, of course, as the buckling of the summer wood progresses, the spring wood also buckles so as to adapt itself to the contour. It is quite evident that in all such cases it is the summer wood that carries most of the compressive load applied parallel to the grain, as might be expected in woods which have pronounced summer wood. When there is no such pronounced difference between summer wood and spring wood—as in birch, maple, and red gum, for example—the material of the various cells more uniformly share the load and the contrast between buckling and crinkling is not so apparent. Over against these cases of wood of almost entire "summer-woodlike" structures,

[8] Robinson, W. Op. cit.

[9] Brush, W. D. A microscopic study of the mechanical failure of wood. U. S. Dept. Agr., Forest Serv., Rev. Forest Serv. Invest. 2: 33-38, illus. 1913.

in which all the cell walls in the regions of failure buckle, stands the example of balsa, on which a few tests have been made. Here the phenomenon of failure could probably better be described as crinkling only, the whole structure being more of the nature of spring wood.

It is the direction in which the offset due to buckling takes place which predetermines the direction in which the region of failure is inclined. If the buckling takes place in a tangential direction, as it nearly always does, then the failure will be inclined on the tangential face. (See fig. 3.) For it is obvious that the least amount of friction and shearing will take place between fibers in buckling when their curvatures fit together most closely, a condition which can occur only when the curvature of one fiber is a little below that of the adjacent one. Hence the zone of a series of such curvatures would assume an angle with the horizontal.

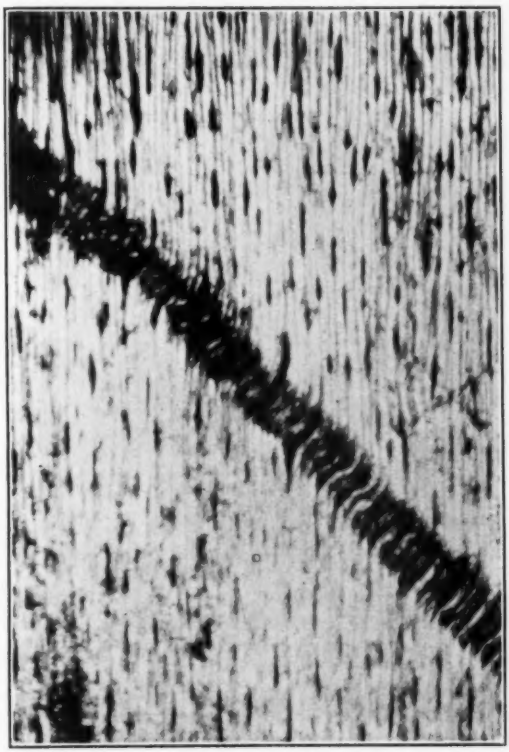

FIG. 3.—Tangential offset in gross compression failures in Douglas fir. Photographed by polarizedlight. × 30

Radial offsets have been found in a few cases in the softwoods, but even then it was in only a very few that the gross failure formed an angle of considerably less than 90° with the vertical on the radial face. Figure 4 illustrates one of the cases with a definitely radial offset, but with the gross failure still almost horizontal, or at an angle of about 90° with the grain. It is noticeable, however, that within each of the summer-wood layers (the lighter-colored bands in the figure) the failure is decidedly at an acute angle. Thus it is possible, evidently, that numerous little parts of the whole failure may follow their own direction over a certain distance, then merge again into the main trend of the failure of which they are parts.

## RÉSUMÉ OF COMPRESSION TESTS

In the entire lot of 324 softwood specimens tested in end compression, only three cases were found in which the failure made any considerable angle with the horizontal on the radial faces, and in the 200 hardwood specimens tested none was found. In the three exceptional cases the angle was much smaller than those usually seen on tangential faces. Only one of the three showed a strictly radial offset, and its abnormal deformation may possibly be explained by the presence of a small knot in the zone of failure. The other two had both tangential and radial offsets. In these two, as well as in eight others which had both tangential and radial offsets, but horizontal failures on radial faces, the radial offsets may have been due to the advanced stage to which the failures were carried in the testing machine.

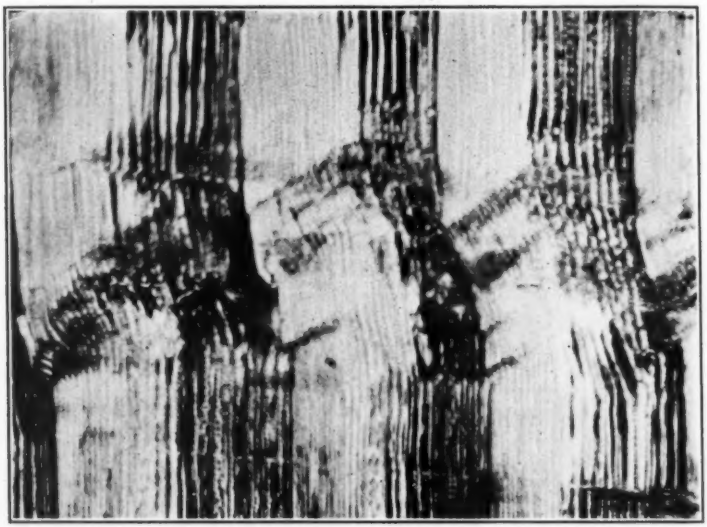

FIG. 4.—Radial offset (unusual) in gross compression failure in Douglas fir. Photographed by polarized light. × 28.5

According to Robinson [10] the behavior of spruce is exceptional, in that it forms a radial offset as a rule. Such a finding was not confirmed here. Of 100 standard-sized pieces of Sitka spruce that were tested in compression parallel to the grain, by far the greater number had a quite normal tangential offset, only three cases showing a composite radial and tangential offset. (These are included in the 10 referred to above.) That either a radial offset or an inclined gross failure on the radial face is quite exceptional in all the woods studied, including Sitka spruce, seems conclusively demonstrated.

Considering a possible relation between the angle of gross failure and density, Thil [11] states that the harder (heavier) the wood, the smaller the angle the failure makes with the vertical.

[10] ROBINSON, W. Op. cit., p. 52, 53, 56.

[11] THIL, A. CONSTITUTION ANATOMIQUE DU BOIS.—ETUDE SUR LES FRACTURES DES BOIS DANS LES ESSAIS DE RÉSISTANCE. Publié par commission des méthodes d'essai des matériaux de construction sous les auspices du Ministère des travaux publics de France. Tome III, rapports particuliers, p. 140–141. Paris. 1900. [Not seen.]

The general angle of the gross failure with the vertical on strictly tangential faces showed the following average values in the softwood and oak specimens tested for this study:

| | Degrees |
|---|---|
| Sitka spruce (dry) | 70 |
| Douglas fir (dry) | 64½ |
| Douglas fir (moist) | 63 |
| Southern yellow pine (dry) | 59½ |
| White oak group (dry) | 57 |

The number of tests of hardwoods other than oak was not large enough to afford a fair average. The results bear out Thil's statement, since the angle is largest in Sitka spruce and smallest in oak, with Douglas fir and yellow pine intermediate, all inversely as the density of the species. The plane of failure was somewhat more definitely marked, and the buckling more gradual, in the harder woods.

For the southern yellow pine, Douglas fir, and oak used in this study, the angle of the gross failure with the vertical was plotted against the specific gravity of each specimen. In oak, especially, the different pieces were of widely different specific gravities, so that the mode of variation could be observed over a fairly representative range. From the diagrams it was concluded that *within a species* there is no controlling relation between the angle of failure and the specific gravity.[12]

## SUPPLEMENTARY TESTS TO DETERMINE EFFECT OF CROSS SECTION

In order to determine whether the relative dimensions of the cross section of rectangular specimens have any influence on the manner of failure, provided the axial length of the test piece is such that bending is practically excluded, a series of tests was performed on red gum, mahogany, ash, Douglas fir, and southern yellow pine. For each species test pieces of the following transverse dimensions, in inches, were prepared: 1¼ by 2½, 1¼ by 1¾, 1¼ by 1½, 1¼ by 1¼, and 1¼ by ⅝. The length of each piece was 4 inches. Figures 5 and 6 show the red-gum specimens after test, with moisture sections cut off and placed above the pieces, showing the direction of the growth rings. Figures 5 and 6 show that in all cases, no matter what the dimensions of the transverse section, the blocks have a tangential offset; the failure makes a definite acute angle with the grain on the tangential face; and on the radial face the failure runs across horizontally, or almost so, all in the regular manner.

## DISCUSSION OF THE MODE OF FAILURE

Many reasons have been advanced by different investigators in an endeavor to explain the typical inclination of the gross failures on tangential faces. Thil [13] attempted to show that the angle of the

[12] P. Jaccard makes the same statement, "qu'il n'existe pas de type de rupture specifique, c'est-à-dire propre à chaque espsce ligneuse . . . " JACCARD, P. ETUDE ANATOMIQUE DE BOIS COMPRIMÉS. Mitt. Schweiz. Centralanst. Forstl. Versuchsw. 10: 57. 1910.

[13] THIL, A. Op. cit.

failures is related to a supposed spiral arrangement of the medullary rays. Supposing the tops of the rays to be naturally arranged along imaginary spirals around the stem, he considered the spirals as lines of least resistance. A careful examination of tangential sections shows, however, that such an arrangement of rays evidently does not exist. This observation is confirmed by Jaccard's remarks upon Thil's article: "One needs only to reproduce by the camera lucida or by photomicrography the distribution of rays on the tangential faces of the test pieces which have been compressed, to be convinced that no constant relation exists between such distribution and the direction of the lines of rupture." The 15 tests made in the present investigation on mahogany (in which the rays are in horizontal rows) gave consistent evidence against Thil's hypothesis, since they produced the same type of offset and inclined failure on the tangential faces as is typical of other woods.

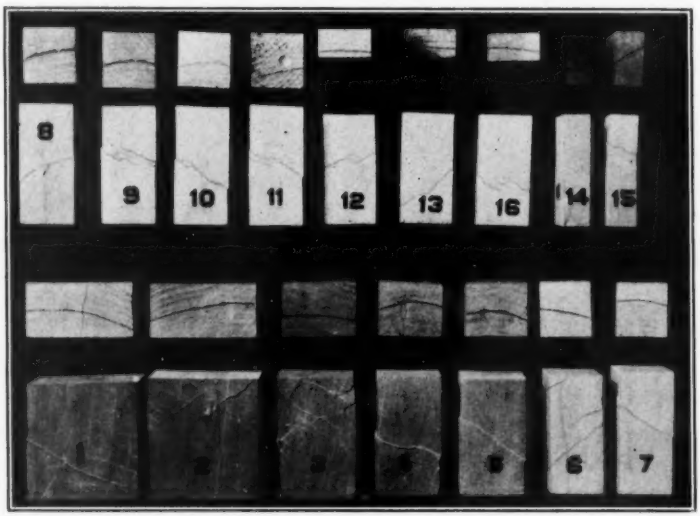


FIG. 5.—Tangential surfaces of red gum, a homogeneous wood, showing inclined failures due to compression parallel to the grain. (The pencil lines across the end surfaces of sections above each specimen indicate the direction of the annual rings)

A somewhat similar arrangement to that supposed by Thil for the rays could be imagined for the wood fibers in a tangential plane in contrast to their frequent horizontal arrangement in radial planes; but here also a study of tangential sections affords no evidence of the fibers being arranged in inclined zones corresponding to the zones of failure.

The fact that in the gross compression failure on the tangential face a separation sometimes is found between the rays and the surrounding fibers probably accounts for the supposition that the junction of ray and fiber forms a weak spot which could therefore be considered as the starting point of the failure. But closer microscopic examination shows that this separation at the rays takes place only after buckling of the fiber material as a whole has progressed

considerably, at which stage the fibers tend to separate from each other as well. Figure 3 shows that in the case of advanced buckling fibers may separate, even when there are no rays in the immediate neighborhood. Moreover, in the comparatively rare cases of radial offsets, it is known that separation of fibers may occur in the radial direction, where the rays could have no weakening influence. In fact, the first steps in the buckling of the fibers take place on too small a scale to be affected by the rays, and manifest no relation to them. It has already been explained [14] in this paper that the origin of failure lies in the giving way of the individual cell wall, and the development of these minute injuries into the later failures has been indicated.

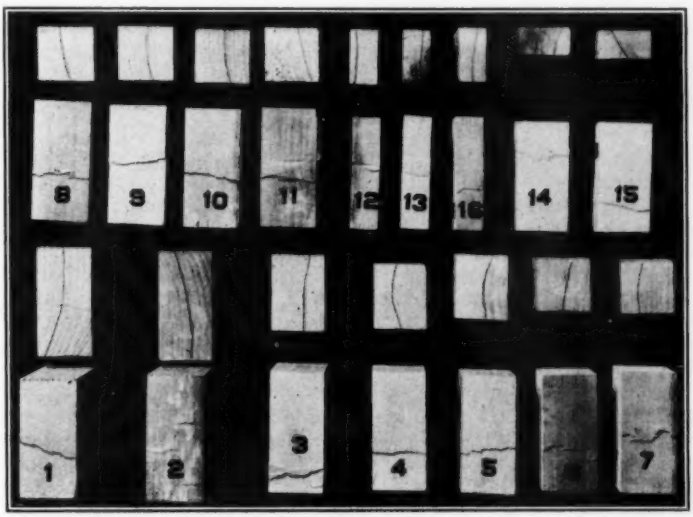


FIG. 6.—Radial surfaces of same blocks as in Figure 5, showing more or less horizontal conformation of failures

Jaccard [15] holds that rupture is determined by points of least resistance in the wood[16] which reduce cohesion and the homogeneity of the wood fibers and which favor their bending and folding. According to Jaccard, the pits in the walls of the tracheids or fibers form such points of weakness. But again the photomicrographs made for the study of initial failures show that evidence for supposing such a relation is lacking, and the argument therefore fails as an explanation of the character or the commencement of the failure.

That nonhomogeneity arising from any structural differences as between spring wood and summer wood is not to be regarded as the explanation of the inclination of the plane of failure in wood subjected to compression is shown by the fact that woods of highly homogeneous structure in this respect—for example, red gum, birch, maple, and

[14] As has also been shown by ROBINSON, W. Op. cit.

[15] JACCARD, P. Op. cit.

[16] In the present paper only perfectly clear material is considered. Jaccard includes the following among his "points of least resistance": "Knots, of which some are very small and do not even appear on the surface of the specimen, by which the straightness of the fibers is markedly altered and their cohesion interrupted."

mahogany—behave in exactly the same manner as less homogeneous woods such as oak, ash, Douglas fir, and yellow pine.

The only remaining known and consistent factor which could possibly exert sufficient influence to account for such almost universal inclination of the failure in a tangential direction must be looked for in the action of the medullary rays. It has already been pointed out that it is neither the spiral arrangement of the rays nor a weak bond between the rays and the wood fibers that can account for the tangential inclination of the failure. It therefore seems reasonable to assume that the cause must lie in the stiffening effect which the rays have radially, this increasing the resistance of the fibers to buckling in that direction and causing them to buckle tangentially, which necessitates the inclination of the failure on the tangential face. This conclusion can, of course, be arrived at only by the process of disproving the possible influence of other factors. It can not be proved directly, since the same piece of wood can not be tested with and without rays.

## CONCLUSIONS

This study corroborates Robinson's statement that slip lines, or slip planes, are the first indication of injury in compression parallel to the grain, but it is doubtful whether they are likewise produced in tension along the grain.

The early or initial failures, consisting principally of numerous localized slip planes, show no such distinctive difference between their radial and tangential aspects as that exhibited by gross failures. Apparently, however, they are sources of zones of weakness within which the buckling of the fibers resulting in gross failures may start more easily than elsewhere.

The gross failure in compression parallel to the grain consists of a buckling of the fibers. The least amount of friction between fibers occurs when the plane of buckling, or failure, is inclined. The inclination of the failure occurs, as a rule, in a tangential direction. The present writer has shown that the only probable explanation of this behavoir is that the medullary rays increase the resistance to buckling in a radial direction, thus causing the line of failure to be inclined on the tangential surface.

# THE IMPORTANCE OF CLEARING THE HYDROLYZED SOLUTION IN THE DETERMINATION OF ACID-HYDROLYZABLE CARBOHYDRATES IN GREEN PLANT TISSUE[1]

By V. H. MORRIS, *Assistant Agronomist (Plant Chemistry)*, and F. A. WELTON, *Associate Agronomist, Ohio Agricultural Experiment Station*

## INTRODUCTION

While making a study of the available literature bearing on the separation and quantitative estimation of the various carbohydrate materials in plant tissue, preparatory to some experimental work, it became apparent that all workers do not follow the same procedure in the manipulation of some of the methods involved.

One such method is the determination of starch and similar substances by weak-acid hydrolysis. In this process some workers omit the step of clearing the solution containing the hydrolyzed material, and others apparently consider it necessary. The more generally accepted method appears to be that of clearing the solution by adding an excess of a solution of either basic or neutral lead acetate solution, deleading with sodium phosphate or some other salt solution, and either filtering the solution or allowing the precipitate to settle overnight before taking an aliquot for the determination of the reducing power.

## OBJECT

When many samples are to be analyzed, it is desirable to eliminate unnecessary steps. In the work undertaken there were nearly 200 of the alcohol-preserved samples of green tissue to be analyzed. In view of the large amount of time and labor required to clear the hydrolyzed solutions, it was thought advisable to make a preliminary study of this step, to the end that the process might be shortened or perhaps eliminated altogether.

## MATERIAL

Among the samples preserved for carbohydrate analysis, eight different kinds of green plant material were represented as follows: Wheat culms, oat culms, blue grass, soy-bean stems, cornstalks, Canada-thistle roots, red-clover roots, and wheat rhizomes. The wheat and oat culm samples were taken at heading time. The blue grass was fresh pasture about 5 inches high. The soy beans were sampled when in bloom. The cornstalks were taken when at about the earing stage. The thistle roots, clover roots, and wheat rhizomes were dug up late in the fall. Two samples of each class of material grown under different environmental conditions were selected so that the results of both samples could be considered fairly typical for that class.

[1] Received for publication Dec. 3, 1925; issued July, 1926. Published with the approval of the Director of the Ohio Agricultural Experiment Station.

## METHODS

### PRESERVATION

In most cases 100 grams of the green tissue was taken for the sample, and after being cut into small pieces ½ to 1 inch long the sample was placed in alcohol of such a strength that the final preserving medium would be 70 per cent, and the whole was heated in a water bath at 78° C. for one hour.

### EXTRACTION

The samples were extracted with boiling 80 per cent alcohol in a large Soxhlet extractor for 8 to 12 hours, after which the residue was dried on a steam plate for several days, then placed in a vacuum oven at 105° C. for 8 hours, and then ground finely.

### HYDROLYSIS

For hydrolysis, 3-gram samples were taken of wheat culms, oat culms, blue grass, and soy-bean stems; 2 grams each of cornstalks, thistle roots, and clover roots; and 1 gram of wheat rhizomes. The samples were weighed into 350 c. c. Kjeldahl flasks, 200 c. c. of 2.5 per cent HCl was added, and the flasks, with small funnels in the necks, were placed in a boiling water bath for two hours. The solutions were then filtered through Gooch crucibles with linen filters, washed well with hot water, and then the filtrates were transferred to 500 c. c. volumetric flasks and made up to volume. Aliquots of 100 c. c. each were transferred to 250 c. c. volumetric flasks, cleared or left untreated, made up to volume, and shaken.

### DETERMINATION OF REDUCING POWER

For the determination of reducing power, a modification of the method of Quisumbing and Thomas [2] was used. A 25 c. c. aliquot of the sugar solution was transferred to a 100 c. c. centrifuge tube, 60 c. c. of Fehling's solution was added, and the tube was heated in an electric water bath for 30 minutes at 80° C. The tube was then centrifuged for 10 minutes, the supernatant liquid was poured off, and the reduced copper was shaken with about 15 c. c. freshly boiled distilled water, and again centrifuged for 10 minutes. The supernatant liquid was again poured off, and the reduced copper was determined by the Bertrand method, titrating with N/20 $KMnO_4$.

## EXPERIMENTAL DATA

A preliminary test was carried out with two samples of wheat culms which had exactly the same amount of polysaccharides present. The generally accepted method of clearing described previously was followed, an excess of neutral lead acetate being added, then deleaded with $Na_2HPO_4$ and allowed to settle overnight. The treatment and results are given in Table 1. The results in all tables are expressed in cubic centimeters of N/20 $KMnO_4$ necessary to titrate the reduced copper.

[2] QUISUMBING, F. A., and THOMAS, A. W. CONDITIONS AFFECTING THE QUANTITATIVE DETERMINATION OF REDUCING SUGARS BY FEHLING SOLUTION. Jour. Amer. Chem. Soc. 43: 1503-1526, illus. 1921.

TABLE 1.—*Comparison of cleared and uncleared aliquots*

| Sample | Unneutralized, uncleared | Neutralized, uncleared | Neutralized, cleared |
|---|---|---|---|
| 1 | 6.4 | 6.3 | 6.2 |
| 2 | 6.3 | 6.4 | 6.3 |

The deleading process is the one that takes the most time, so it was decided to determine whether the lead acetate could be added drop by drop until complete precipitation and coagulation was obtained, without adding any excess. Since the point of such complete precipitation is not very sharp, an additional amount of 1 c. c. of the lead solution was added to a second aliquot without subsequent deleading. The results of this procedure are given in Table 2.

TABLE 2.—*Effect of clearing without excess of lead solution*

| Sample | Unneutralized, uncleared | Neutralized, plus lead acetate to cause coagulation | Neutralized, plus 1 c. c. excess lead acetate |
|---|---|---|---|
| 3 | 4.8 | 4.6 | 4.5 |

Apparently this method of clearing does not give results materially different from the check; in fact, an excess of the lead solution may be added without affecting the results.

A group of four samples of different plant tissues was then used in further testing this method of clearing, adding the lead acetate drop by drop until no more precipitation was observed. The results are given in Table 3.

TABLE 3.—*Further test of clearing without excess of lead solution*

| Sample | Unneutralized, uncleared | Neutralized, cleared without excess of lead solution |
|---|---|---|
| Soy beans | 8.9 | 8.9 |
| Thistle roots, No. 1 | 17.1 | 17.4 |
| Thistle roots, No. 2 | 15.1 | 15.3 |
| Clover roots | 13.1 | 13.4 |

In three tables given thus far, there is no significant difference between the check aliquot (that left unneutralized and uncleared) and the cleared aliquot.

In order to test this point further, and also to determine whether there was any difference between different kinds of plant material with respect to the necessity for clearing the hydrolyzed solution, eight classes of plant tissue, including the two different samples of each class, were hydrolyzed. The treatment of the different aliquots and the results are given in Table 4.

TABLE 4.—*Comparison of eight kinds of plant tissue with respect to clearing the hydrolyzed solution*

| Sample | Laboratory No. | Unneutralized, uncleared | Neutralized, uncleared | Neutralized, cleared without excess | Neutralized, cleared with excess lead plus $PO_4$ |
|---|---|---|---|---|---|
| Wheat culms | 238 | 8.1 | 8.3 | 8.3 | ---- |
| Do | 239 | 10.0 | 10.1 | 10.0 | 10.1 |
| Oat culms | 274 | 8.3 | 8.3 | 8.2 | 8.0 |
| Do | 275 | 8.4 | 8.2 | 8.2 | 8.4 |
| Blue grass | 328 | 11.7 | 11.7 | 11.4 | 11.1 |
| Do | 329 | 8.5 | 8.5 | 8.5 | 8.4 |
| Soy-bean stems | 349 | 8.2 | 8.2 | 8.0 | 8.1 |
| Do | 350 | 8.8 | 8.8 | 8.7 | 8.8 |
| Cornstalks | 358 | 8.2 | 7.5 | 7.8 | 7.9 |
| Do | 360 | 7.7 | 7.7 | 7.7 | 7.5 |
| Canada-thistle roots | 363 | 19.3 | 18.7 | 18.9 | 18.7 |
| Do | 364 | 17.7 | 17.4 | 17.1 | 17.4 |
| Red-clover roots | 371 | 15.8 | 15.8 | 15.4 | 15.3 |
| Do | 372 | 15.4 | 15.0 | 15.0 | 14.9 |
| Wheat rhizomes | 379 | 6.2 | 6.2 | 6.2 | ---- |
| Do | 380 | 5.7 | 5.9 | 5.5 | ---- |

With a very few exceptions, apparently the same result is obtained whether the hydrolyzed solution is cleared or not, and, if cleared, it is not necessary to add an excess of the lead solution and then delead. Low or high results on one aliquot out of the four of each sample were obtained in four cases. These results were obtained each with a different treatment, and in every case the other three aliquots checked among themselves, indicating that probably the error was due to some step in the procedure, such as insufficient shaking of the flask after making up to volume, rather than to the effect of the treatment.

### EFFECT OF REACTION OF SOLUTION

The importance of the reaction of the hydrolyzed solution when the lead acetate solution is added has not been very strongly emphasized in published methods. It is very important that the reaction of the solution be kept on the acid side. The addition of lead acetate to a neutral solution results in shifting to an acid reaction, since lead acetate is an acid salt. On the other hand, the addition of a fairly strong basic salt like $Na_3PO_4$ in deleading changes the reaction to alkaline while there is still an excess of lead.

The effect of the alkaline reaction obtained in this way is shown in Table 5, in which the results obtained with several of the samples, keeping one aliquot of the solution acid, are compared with another aliquot of the same solution allowed to become alkaline as suggested above. The solutions were all cleared with lead acetate, adding an excess and deleading with the phosphate solution.

TABLE 5.—*Effect of reaction of hydrolyzed solution*

| Sample | Laboratory No. | Cleared with excess lead, acid reaction | Cleared with excess lead, alkaline reaction |
|---|---|---|---|
| Wheat culms | 239 | 10.1 | 8.6 |
| Oat culms | 274 | 8.0 | 6.8 |
| Do | 275 | 8.4 | 6.8 |
| Blue grass | 328 | 11.1 | 10.5 |
| Do | 329 | 8.4 | 7.8 |
| Soy-bean stems | 350 | 8.8 | 8.4 |
| Cornstalks | 358 | 7.9 | 7.6 |
| Do | 360 | 7.5 | 7.2 |
| Canada-thistle roots | 363 | 18.7 | 16.9 |
| Do | 364 | 17.4 | 16.2 |
| Red-clover roots | 371 | 15.3 | 14.9 |
| Do | 372 | 14.9 | 13.9 |

## DISCUSSION

The advantages of being able to determine, without previous clearing, the reducing power of the solution obtained in the determination of the weak-acid-hydrolyzable carbohydrates, are very obvious. The saving in time and labor is considerable.

The only apparent disadvantage of this procedure is that with some plant materials the precipitate of cuprous oxide obtained is yellowish brown and is in a more finely divided state. The use of the centrifuge in determining the amount of the oxide has a decided advantage over any filtration procedure, on account of the danger of some of the more finely divided particles passing through the filtering medium. The size of the copper particles does not make any real difference in centrifuging, because the smallest crystals are thrown down readily by centrifugal force.

## SUMMARY

The data obtained in the experimental work reported in this paper indicate that with alcohol-preserved samples of green plant tissue of the kinds used in this experiment it is unnecessary to clear, or even neutralize, the hydrolyzed solution before determining the reducing power; and that it is essential that the reaction of the hydrolyzed solution be kept on the acid side in the presence of the lead solution.

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